University of Alberta

Late Paleocene (Tiffanian) mammal-bearing localitites in superposition, from near Drumheller, Alberta

by

Teresa Elise MacDonald ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

Department of Zoology

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Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Late Paleocene (Tiffanian) mammal-bearing localities in superposition from near Drumheller, Alberta** submitted by **Teresa Elise MacDonald** in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

The Hand Hills West locality consists of two fossiliferous horizons in superposition, exposed along the same roadcut in southern Alberta. These two layers (here referred to as the Upper Level and Lower Level) are late Paleocene (Tiffanian) in age. The two horizons in superpositional relationship permit comparison between two faunal assemblages of different ages from one geographical area.

The recovery of *Plesiadapis rex* and *Ectocion cedrus* from the Upper Level indicates an age of middle Tiffanian (Ti3). This zone extends from 61.2 to 58.3 million years ago, for a duration of 2.9 million years. Diagnostic biostratigraphic evidence has not been recovered from the Lower Level. Based on palynostratigraphic and magnetostratigraphic evidence, the Lower Level represents an age of early Tiffanian (Ti2). This zone extends from 61.8 to 61.2 million years ago, for a duration of 0.6 million years. There is a disconformity below the Upper Level which precludes the determination of the precise amount of time between the two levels. Estimated sedimentation rates for the Paskapoo Formation suggest that the minimum amount of time represented between the two levels is approximately 293,000 years.

Fossils recovered from the Hand Hills West locality extend the geological time ranges of the plesiadapiform primates *Elphidotarsius wightoni* and *Nannodectes gidleyi* into the early Tiffanian, the pentacodontid *Bisonalveus* sp., cf. *B. browni* and the multituberculate genus *Baiotomeus* into the middle Tiffanian. The first record of the first upper incisor of *Ignacius frugivorus* and the first lower incisor of *Nannodectes simpsoni*

may be represented from the Upper Level. The first record of the lower canine of Carpodaptes sp., cf. C. hazelae is represented from the Lower Level.

The faunal composition of the Upper Level and Lower Level are similar at the generic and often specific levels. The differences observed between the samples are due primarily to taphonomic and sampling bias.

The faunal composition of the Hand Hills West locality does not differ significantly from other localitites in western Canada, and it reinforces the similarity between assemblages in northern North America and Eurasia, thus supporting the hypothesis of faunal interchange between these regions.

Faunal turnover patterns indicate a relatively stable generic richness in the late Paleocene (Tiffanian) of North America. The generic richness of Tiffanian localities in western Canada does not differ significantly from those in Montana and Wyoming. However, the species diversity of Tiffanian localities in western Canada is higher than in Montana and Wyoming. The significance of this higher diversity is as yet not clear. The importance of western Canada as one of the primary routes of intercontinental exchange lends itself to questions of faunal changes and turnover patterns. Further samples from poorly known localities and intervals are necessary to document the faunal turnover patterns of western Canada and to compare these patterns to those reported from the United States.

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ABBREVIATIONS AND DEFINITIONS

Institutions:

AMNH - American Museum of Natural History, New York

CM - Carnegie Museum of Natural History, Pittsburgh

PU - Princeton University Museum, Princeton

UALVP - Laboratory of Vertebrate Paleontology, University of Alberta, Edmonton

UMCP - Museum of Paleontology, University of California, Berkeley

UM - Museum of Paleontology, University of Michigan, Ann Arbor

USNM - United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

UW - Geological Museum, University of Wyoming, Laramie

Statistics:

CV - Coefficient of variation

M - Mean

N - Sample size

OR - Observed range

P - Parameter

SD - Standard deviation

Dentition:

I, i - Upper or lower incisor, respectively

D, d - Upper or lower deciduous tooth, respectively

P, p - Upper or lower premolar, respectively

M, m - Upper or lower molar, respectively

Measurements (excluding multituberculate p4's):

L - Maximum length across tooth

W - Maximum width of tooth

AW - Trigonid width

PW - Talonid width

Measurements (multituberculate p4's):

H - The distance between the baseline and the first serration.

L - The distance along the baseline extending from the anterior end of the blade to the point where the posterior basal cuspule intersects the posterior margin.

W - maximum transverse width of the blade at the baseline.

Definitions of terms used in text are as follows:

cf. - used to indicate tentative identication of specimens

1.0 INTRODUCTION

1.1 LOCATION

Discovered in 1984, by D.E. Schowalter (Royal Tyrrell Museum of Paleontology, Drumheller, Alberta), the Hand Hills West locality is in the northern section of the Hand Hills area, SE1/4S21 T30 R17 W4, approximately 1,050 metres above sea level (Fox 1990) (Figure 1). The roadcut exposes Paleocene age pale gray to buff shales and siltstones which underlie younger Tertiary gravels (Hand Hills conglomerate, Storer 1978). The Upper Level is near the top of the section in a thin brown to dark gray shale, in the highest unconsolidated sand just below the Hand Hills conglomerate. This sand unit is scoured down into the paler shales beneath, producing a shallow disconformity (Fox 1990). In August 1986, R.C. Fox (University of Alberta, Department of Biological Sciences), discovered the Lower Level, approximately 200 metres northeast and 22 metres below the Upper Level. The Lower Level is near the base of the exposed section in uniform, fine-grained, dark brown and black shale (Fox 1990).

1.2 GEOLOGY

The Hand Hills are an erosional remnant plateau located approximately 25 km northeast of Drumheller, Alberta (Figure 1). They are the highest topographic feature of southcentral Alberta, approximately 1,064 metres at the northwestern range and 213 metres above the surrounding prairie (Storer 1976). The south section of the Hand Hills exposes in ascending order, the Whitemud, Battle, and Scollard formations. The northern section exposes in ascending order, the Scollard, Paskapoo and Hand Hills formations. These formations include Cretaceous, Paleocene, Miocene, Pliocene, and Pleistocene sediments (Lerbekmo and Demchuk et al. 1992). In the northern section of the Hand Hills plateau, the Paskapoo Formation is eroded disconformably by remnants of younger Tertiary sediments, known as the Hand Hills Formation, Hand Hills Gravels, or Hand Hills Conglomerate (Storer 1978). The Tertiary sediments have been reworked by glacial activity, resulting in a mixed temporal and stratigraphic relationship (Storer 1976). The gravels are correlated with the Flaxville Plain of northeastern Montana (Warren 1939), and range from Miocene to Pleistocene in age (Storer 1978). The Hand Hills West locality is within the Paskapoo Formation. The lower boundary of the Paskapoo Formation has been subject to some debate (Tyrrell 1887, Carrigy 1970, 1971, Gibson 1977), but is generally considered to be at the base of the first prominent sandstone above the major coal seam of the Coalspur Coal Zone in the foothills (Jerzykiewicz in press, Demchuk and Hills 1991). The Haynes Member constitutes the lower part of the Paskapoo Formation (lower Paleocene) and it is characterized by thick sandstone (Demchuk and Mills 1991). The thick sandstone characteristic of the Haynes Member is poorly developed in the Hand Hills (Demchuk and Mills 1991). The Lacombe Member forms the upper part of the Paskapoo Formation (middle and upper Paleocene) and is characterized by argillaceous and carbonaceous sediments (Demchuk and Mills 1991). According to Demchuk and Mills (1991), the lowermost portion of the Lacombe Member may extend into the Hand Hills; this correlation is based on lithological and palynological evidence. The Hand Hills West locality is late Paleocene (Tiffanian) in age and the faunal composition of the Upper Level closely resembles other localities of the same age that are in the Lacombe Member. This observation supports Demchuk and Mills' (1991) suggestion that the Lacombe Member extends into the Hand Hills.

1.3 MAGNETOSTRATIGRAPHY

Magnetostratigraphic evidence is important as an independent means of determining the relative age of the two levels in the Hand Hills West locality. The south section of the Hand Hills includes magnetostratigraphic zones 30, 29R, and 29 (Lerbekmo et al. 1995). The northern section of the Hand Hills, which includes the Hand Hills West locality, includes magnetostratigraphic zones 30, 29R, 29, 28R, 27, and 26R (Lerbekmo et al. 1995). There is a "Sub-Paskapoo" disconformity in the Hand Hills representing approximately a two million year hiatus (Demchuk 1990, Lerbekmo et al. 1995). This disconformity spans zones 28R, 28, and 27R and coincides with the base of a 3 metre thick sandstone in the Paskapoo Formation. The 26R zone includes the earliest Tiffanian (Ti1), the early Tiffanian (Ti2) and the early part of the middle Tiffanian (Ti3) (Table 1). The lower part of the 26 zone includes the middle Tiffanian (Ti3), and the upper part includes the early late Tiffanian (Ti4) (Lerbekmo and Demchuk et al. 1992). Polarity data are not available for the Upper Level of the Hand Hills West locality. The Lower Level is located low in the youngest reversed zone, near the base of 26R (Lerbekmo et al. 1995).

Thus, based on magnetostratigraphic evidence, the age of the Lower Level is no older than earliest Tiffanian (Ti1) and no younger than middle Tiffanian (Ti3).

1.4 PALYNOSTRATIGRAPHY

Demchuk (1987, 1990) recognized six Paleocene palynofloral zones in the central Alberta Plains, extending from the Cretaceous-Tertiary boundary in the Scollard Formation to the top of the Paskapoo Formation (Table 1). These zones correspond closely with the zones recognized by Nichols and Ott (1978) for the Wind River Basin, Wyoming (Demchuk 1990). The P3 (Aquilapollenites spinulosus) palynofloral zone ranges in age from the late Torrejonian to the early middle Tiffanian. The P4 (Caryapollenites wodehousei) palynofloral zone includes the middle and late Tiffanian (Demchuk 1987, 1990).

Samples taken from the Lower Level fall within the P3 palynofloral zone. The lack of pollen in the Upper Level precludes recognition of a palynofloral zone. Late Paleocene (middle Tiffanian) localities on the Blindman River and Red Deer River in central Alberta, the mammalian faunal assemblages of which are comparable to those from the Hand Hills Upper Level, are within Demchuk's P4 palynofloral zone (Demchuk 1990).

1.5 BIOSTRATIGRAPHY

The late Paleocene (Tiffanian and early Clarkforkian) is divided into five biostratigraphic zones (Table 2), based on the lineage of the plesiadapiform primate Plesiadapis (Gingerich 1976). The recovery of Plesiadapis rex from the Upper Level indicates an age of Ti3 (middle Tiffanian) for this faunal assemblage. The phenacodontid condylarth Ectocion is also suggested to be a biostratigraphically significant genus (Thewissen 1990) (Table 2). The presence of Ectocion cedrus in the Upper Level further supports an age of middle Tiffanian for this horizon (Thewissen 1990). Diagnostic plesiadapid and phenacodontid material has not been recovered from the Lower Level. However, the presence in this level of the plesiadapiform primate Ignacius is of interest. Ignacius fremontensis is recorded from Alberta localities that are earliest Tiffanian (Ti1) in age, and Ignacius frugivorus is found in younger localities in Alberta, Montana, and Wyoming that are early Tiffanian (Ti2) and middle Tiffanian (Ti3) in age. The recovery of the latter species from the Lower Level indicates that this level is likely younger than earliest Tiffanian (Ti1) in age.

1.6 DEPOSITIONAL ENVIRONMENT

The Upper Level is located near the top of the section at the roadcut, in a thin, carbonaceous, shaly unit near the base of the highest thin (0.5 metres) unconsolidated sand, just below the Hand Hills Conglomerate (Fox 1990); the fossils occur in uniform, fine-grained, poorly lithified sandstone. This pattern of sedimentation is consistent with a channel fill deposit (i.e., the result of abandoned channels or reduced slope) (Allen 1965, Behrensmeyer et al. 1979). The absence of coarse sediments eliminates an oxbow lake, crevasse splay, or point bar deposit. The Lower Level is in dark brown and black silt, slightly compacted and lithified, and is characterized by uniform, fine-grained, silty sediments that are consistent with a channel fill or floodplain deposit (i.e., the result of periodic flooding) (Allen 1965, Behrensmeyer et al. 1979). Channel fills are similar to floodplain deposits, and are usually distinguished by the presence of bedding, and some coarse material. There are no distinctive sedimentary structures associated with these deposits, other than occasional mudclasts in the surrounding sediments. The Upper Level is characterized by relatively coarser sands, and the Lower Level is characterized by fine silts. It is on this basis that the Upper Level is considered to be a channel deposit and the Lower Level to be a floodplain deposit.

2.0 METHODS AND DENTAL TERMINOLOGY

Specimens were collected by quarrying. Matrix was collected by field parties of the University of Alberta Laboratory for Vertebrate Paleontology from 1984 to 1987 (Upper Level), and 1986 and 1994 (Lower Level). Matrix from both levels was screen-washed by D.W. Krause's (unpublished) method. After drying, the screened material was sorted under a dissecting microscope and identifiable mammalian teeth were removed for study.

All measurements of mammalian teeth are in millimeters and were estimated to the nearest 0.1mm using a Wild M-3B zoom binocular microscope with 20 magnification oculars. An ocular micrometer disc divided into 0.1 intervals was inserted into the microscope and calibrated against a millimeter scale. Measurements of multituberculate p4's follow Novacek and Clemens (1977). Nomenclature for multituberculate p4's follows Krause (1977), Sloan (1981), and Johnston and Fox (1984). Nomenclature and measurements for multituberculate dentitions other than p4 follow Simpson (1937a), Jepsen (1930), and Krause (1987). The illustrations of specimens were made using a camera lucida attached to a Wild M-3 binocular microscope.

Measurements of therian teeth follow Clemens (1966) and Gingerich and Winkler (1985). Dental terminology for therians follows that of Van Valen (1966), as modified by Szalay (1969) and Schiebout (1974). Carnivoran nomenclature follows MacIntyre (1966). The terms pre-, sub-, and semimolariform are as used by Krishtalka (1976).

Identifications were based on published descriptions and figures and on comparative material in the University of Alberta Laboratory for Vertebrate Paleontology collections.

The relative abundance of the taxa follows Badgley (1986a), who proposed that in fluvial deposits containing isolated specimens, the number of individuals equals the number of specimens.

Statistics performed include Whittaker's and Pielou's indices of species evenness, Shannon-Weiner and Simpson's indices of heterogeneity, faunal completeness and standing generic richness indices (Maas and Krause 1990, Maas et al. 1995) (see Appendix).

3.0 SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus 1758

Subclass Allotheria Marsh 1880

Order Multituberculata Cope 1884

Suborder Ptilodontoidea Sloan and Van Valen 1965

Family Neoplagiaulacidae Ameghino 1890

Genus Mimetodon Jepsen 1940

Mimetodon silberlingi (Simpson 1935)

(Figure 4a,b; Table 3)

Holotype: USNM 9798, left dentary fragment with i1, p4-m2.

Type locality: Gidley Quarry, upper Lebo Formation, Crazy Mountain Field, Sweetgrass County, Montana.

Known age and distribution: Late Torrejonian (middle Paleocene) of Montana (type locality [Simpson 1935a, 1937]), and Wyoming (Rock Bench Quarry, Fort Union Formation, Polecat Bench [Jepsen 1940], Swain Quarry, Fort Union Formation, Washakie Basin [Sloan in Holtzman 1978]); earliest Tiffanian (late Paleocene) of Wyoming (Keefer Hill locality ["Shotgun Local Fauna"], Fort Union Formation, Wind River Basin [Sloan in D.E. Russell 1967]) and Alberta (Cochrane 2 locality, Porcupine Hills Formation, Cochrane [Youzwyshyn 1988, Fox 1990]); early Tiffanian of Texas (localities 40147 and 41365, Black Peaks Formation, Big Bend National Park [Schiebout 1974]); middle

Tiffanian of Alberta (UADW-1 and UADW-2 localities, Paskapoo Formation, Blindman River [Fox 1984a, 1990], Joffre Bridge Roadcut, Paskapoo Formation, Red Deer River [Fox 1990], Birchwood locality, Paskapoo Formation, Drayton Valley [M.W. Webb in prep.]); late Tiffanian of Montana (Olive locality, Tongue River Formation, Powder River Basin [Sloan in D.E. Russell 1967]), Alberta (Police Point locality, Ravenscrag Formation, Cypress Hills [Krishtalka 1973]; Swan Hills site 1, Paskapoo Formation, Swan Hills [Stonley 1988], and Saskatchewan (Roche Percée Local Fauna, Ravenscrag Formation [Krause 1977]).

Referred specimens: UALVP 35227, M2; 34949, 35225, 35226, 35228, p4s.

Horizon: Hand Hills West, Upper Level and Lower Level.

Description:

M2. - The cusp formula of this specimen is 3:3:1. M2 of this species has been adequately described and figured by Krause (1977).

p4. - These specimens have 10 serrations, the fourth is the highest, with labial and lingual bifurcation ridges from the first serration on a relatively low crown. The distance from the anterobasal concavity to the first serration is slightly less than 1/2 the total length of the blade. The posterior slope is steeper than the anterior, the posterior basal cuspule forms a well-developed shelf, the anterolingual extension of the cuspule extends straight along the base of the enamel, and the exodaenodont lobe is peaked ventrally.

Discussion:

There are no significant differences between the samples from the Upper Level and the Lower Level.

This species is known from the late Torrejonian to the late Tiffanian, with a wide geographic distribution from northern Alberta to Texas.

Genus *Mesodma* Jepsen 1940

Mesodma pygmaea Sloan 1987

(Figure 5a-d; Table 4)

Holotype: AMNH 35298, left dentary fragment with p4-m2.

Type locality: Gidley Quarry, upper Lebo Formation, Crazy Mountain Field, Sweetgrass County, Montana.

Known age and distribution: Late Torrejonian (middle Paleocene) of Montana (type locality) and Wyoming (Rock Bench Quarry, Fort Union Formation, Polecat Bench [Sloan *in* Holtzman 1978, Sloan 1987], Swain Quarry, Fort Union Formation, Washakie Basin [Sloan *in* Holtzman 1978, Sloan 1987]); latest Torrejonian of Montana (Medicine Rocks I locality, Tongue River Formation, Carter County [Sloan 1987]); earliest Tiffanian (late Paleocene) of Wyoming (Keefer Hill [Shotgun] locality, Fort Union Formation, Winder River Basin, Fremont County [Sloan *in* Holtzman 1978]); early Tiffanian of Wyoming (Saddle locality, Fort Union Formation, Bison Basin [Sloan in Holtzman 1978, Sloan 1987]), and Alberta (Cochrane 2 locality, Porcupine Hills Formation, Cochrane [Youzwyshyn 1988]); middle Tiffanian of North Dakota (Brisbane locality, Tongue River Formation, Grant County [Holtzman 1978]), and Alberta (UADW-1 and UADW-2 localities, Paskapoo Formation, Blindman River [Fox 1984a, 1990]); late Tiffanian of Saskatchewan (Roche Percée Local Fauna, Ravenscrag Formation [Krause 1977]).

Referred specimens: UALVP 35219, 35221, 35223, 35220, M2s; 34948, 35218, 35222, 35224, p4s; 34951, 34952, m1s; 34953, m2.

Horizon: Hand Hills West, Upper Level and Lower Level.

Description and discussion:

M2. - The cusp formula of these specimens are 3:3:1. The M2 has been adequately described and figured by Krishtalka (1973) and Krause (1977).

p4. - These specimens have 12 serrations, the fourth or fifth serration appears to have been the highest (top portion of these cusps is missing), and the anterior portion of the blade is peaked to form an incipient ridge. The distance from the anterobasal concavity to the first serration is less than 1/3 of the total length, the posterior basal cuspule forms a well-developed shelf, and the exodaenodont lobe is more rounded than peaked ventrally.

m1. - The cusp formula is 7:4. These specimens are similar in morphology and size to material of this species described and figured by Krishtalka (1973), Krause (1977), and Sloan (1987).

m2. - UALVP 34953 is an isolated lower right second molar. It is morphologically identical to specimens of Mesodma pygmaea from the late Tiffanian Roche Percée locality described and figured by Krause (1977). The Roche Percée and Hand Hills West material differs from m2 of M. pygmaea from the late Torrejonian Gidley Quarry (Sloan 1987) and late Tiffanian Police Point Locality (Krishtalka 1973) in being slightly smaller, with a cusp formula of 4:2 rather than 3:2 (Krause 1976).

Mesodma sp. P (see Krishtalka 1973)

(Figure 6)

Holotype: not designated.

Type locality: UAR-1 Ravenscrag Formation, Alberta.

Known age and distribution: Early Tiffanian of Alberta (Cochrane 2, Porcupine Hills Formation, Cochrane [Youzwyshyn 1988]); middle Tiffanian of Saskatchewan (late Paleocene) (Roche Percée, Ravenscrag Formation [Krause 1977]), Montana (Gidley Quarry, upper Lebo Formation, Crazy Mountain Field, Sweetgrass County [Krishtalka 1973]) and Wyoming (Shotgun Member, Shotgun Formation, Fort Union Formation, Badwater Creek locality, Shotgun Member, Fort Union Formation [Krishtalka 1975]); late Tiffanian of Saskatchewan (Police Point locality, Ravenscrag Formation [Krishtalka 1973]) and Alberta (Cypress Hills locality, Paskapoo Formation [Krishtalka 1973]).

Referred specimen: UALVP 34964, P4.

Horizon: Hand Hills West, Upper Level.

Description:

P4. - UALVP 34964 is an isolated right upper fourth premolar. This specimen (L=2.0mm, W=0.8mm) has an elongated occlusal view, is somewhat sigmoidal in shape, with a moderate bulge extending anterolabially. The penultimate cusp is the highest in the lingual row, and there are two laterally compressed cuspules on either side of a centrally located depression on the posterior end of the tooth. The cusp formula of this specimen is 2:7:0, with one fewer cusp in the labial row than in P4s of Mesodma sp. P from the late Tiffanian Roche Percée locality (3:5-7:0, Krause 1977), and within the range from the late Tiffanian Police Point locality (2-3:5-7:0, Krishtalka 1973). UA 10942 from the Police Point locality (Krishtalka 1973) has a small cusp posterior and dorsal to the tallest cusp of the middle row that was not included in the cusp formula; this cusp is absent on this specimen. This specimen is morphologically similar to the P4 of Mesodma sp. P from the late Tiffanian of Alberta and Saskatchewan. It most closely resembles the P4 of Mesodma sp. P from the Police Point locality (Krishtalka 1973) in terms of size and cusp formula.

Discussion:

Sloan (1987) synonymized Mesodma sp. P from the late Tiffanian of Saskatchewan (Roche Percée locality, Krause 1977) and Alberta (Police Point locality, Krishtalka 1973), and Mesodma sp. from the middle Tiffanian of North Dakota (Brisbane locality, Holtzman 1978) with Mesodma pygmaea. However, Youzwyshyn (1988) recognized Mesodma sp. P from the earliest Tiffanian Cochrane 2 locality as a distinct species from M. pygmaea. The isolated P4 from the Hand Hills West, Upper Level, in comparison with the Roche Percée and Police Point specimens, support the recognition of Mesodma sp. P as a distinct species from Mesodma pygmaea.

Mesodma sp.

(Figure 7)

Referred specimen: UALVP 34950, p4.

Horizon: Hand Hills West, Upper Level.

Description and discussion:

UALVP 34950 is an isolated lower left fourth premolar. It has 14 serrations; the fifth serration is the highest; the distance from the anterobasal concavity to the first serration is less than 1/3 the total length of the blade; and the first and second serrations bifurcate labially and lingually. These features are consistent with the generic diagnosis of Mesodma (Clemens 1964, Krause 1977).

This specimen is similar to the p4 of Mesodma pygmaea in terms of profile, higher than the p4 in M. formosa and M. thompsoni, but much larger (L=4.1mm, W=1.2mm, H=1.2mm) with more serrations than in either M. pygmaea or M. prolis (undescribed new species, see Stonley 1988). The blade is high anteriorly, sharply decreasing in height toward the posterior end of the blade. The posterior basal cuspule is well developed, with the enamel ridge of the cuspule continuing dorsally, along the side of the blade, rather than directly anterior and horizontal along the base of the blade, as in M. pygmaea.

Ectypodus Matthew and Granger 1921

Ectypodus sp., cf. E. szalayi Sloan 1981

(Figure 8a, b)

Holotype of Ectypodus szalayi: AMNH 35536, left and right associated dentaries, each with i1-m2.

Type locality: Gidley Quarry, upper Lebo Formation, Crazy Mountain Field, Sweetgrass County, Montana.

Known age and distribution of Ectypodus szalayi: Middle Torrejonian (middle Paleocene) of New Mexico (KU locality 13, Nacimiento Formation, Kutz Canyon, San Juan Basin [Sloan 1981a]); late Torrejonian of Wyoming (Swain Quarry, Fort Union Formation, Washakie Basin, Carbon County [Sloan 1981a]) and Montana (type locality [Sloan 1981a]).

Referred specimens: UALVP 34961, 34962, 34963, 34956, 34957, P4s; 34959, 34960, p4s.

Horizon: Hand Hills West, Upper Level.

Description and discussion:

P4. - Cusp formula 0:2:6. The dimensions are (L=1.7-1.8mm, W=0.64-0.82mm). The P4s are trenchant, the anterior slope is straight, the posterior slope is straight to slightly concave, and the posterior basal cuspule is weakly developed. The cusps of the lingual row are approximately equal in height and in line, and the second cusp of the labial row is significantly larger than the first cusp, with the cusps decreasing in height further posteriorly. The anterior most cuspule of the labial row is located directly across from the first cusp of the lingual row.

The straight anterior slope of this specimen is similar to the P4 of E. sp., cf. E. powelli from the Late Tiffanian Roche Percée locality, but differs in being smaller, with fewer cusps in the lingual row (0:3:7; see Krause 1977). These specimens are similar to described material referred to Ectypodus sp. from the middle Tiffanian of North Dakota (see Holtzman 1978), but are slightly smaller, and have fewer cusps in the labial and lingual rows. The Hand Hills West specimens are most similar in terms of morphology to the P4 of E. sp., cf. E. szalayi from the earliest Tiffanian Cochrane 2 locality (see Youzwyshyn 1988), but are slightly smaller.

p4. - The lower fourth premolars are both incomplete. The enamel is worn, so the description provided is based on a composite of the two p4s. The profile is high and arcuate, and the anterior and posterior slopes are straight. There appear to be 10 serrations, and the third or fourth cusp appears to have been the highest. The posterior basal cuspule is moderately developed, and the striations are strong labially. The distance from the anterobasal concavity to the first serration is less than 1/3 the total length of the blade.

The dimensions of these specimens (composite) are (L=2.5mm, H=2.0mm, W=0.76). The length is within the size range for the p4 of E. szalayi from the late

Torrejonian Gidley Quarry (2.6mm-2.8mm) (Sloan 1981a), but the exodaenodont lobe is narrower and extends further labially, as in E. powelli (Jepsen 1940) and E. sp., cf. E. szalayi from the earliest Tiffanian Cochrane 2 locality (see Youzwyshyn 1988). These specimens are smaller than the p4s of E. powelli (Jepsen 1940), E. sp., cf. E. powelli from the late Tiffanian Roche Percée Local Fauna (see Krause 1977), and Ectypodus sp. from the middle Tiffanian Brisbane locality (see Holtzman 1978). There are fewer serrations than in E. hunteri, E. hazeni and E. musculus, within the known range for E. powelli, but the profile is not as high as in E. powelli.

These specimens are most similar in terms of morphology to the p4 of, E. powelli (Sloan 1981a) from the late Torrejonian Gidley Quarry, and the p4 of Ectypodus sp., cf. E. szalayi from the earliest Tiffanian Cochrane 2 locality (see Youzwyshyn 1988), but are slightly smaller. The morphology of these specimens is intermediate between E. szalayi and E. powelli (Sloan 1981a).

Ectypodus sp.

Referred specimens: UALVP 35230, 35231, M's; 35229, p4.

Horizon: Hand Hills West, Lower Level.

Description and discussion:

This material is highly fragmented and moderately worn; therefore, identification below the genus level is not possible. E. szalayi is known from the middle and late Torrejonian (Sloan 1981a), E. sp., cf. E. szalayi from the earliest Tiffanian and middle Tiffanian (see Youzwyshyn 1988, Fox 1990), and E. powelli and E. sp., cf. E. powelli from the middle and late Torrejonian, and middle and late Tiffanian (Jepsen 1940, Krause 1977, Sloan 1981a, Fox 1990). Based on the age of early Tiffanian for the Lower Level, and the recovery of E. sp., cf. E. szalayi from the Upper Level, these specimens are likely referrable to E. szalayi or E. sp., cf. E. szalayi.

Genus Neoplagiaulax Lemoine 1882

Neoplagiaulax sp., cf. N. hazeni Jepsen 1940

(Figure 9a, b; Table 5)

Holotype of Neoplagiaulax hazeni: PU 14432, right maxillary fragment with incomplete P3 and P4-M2.

Type locality: Princeton Quarry, Polecat Bench Formation, Park County, Wyoming.

Known age and distribution of Neoplagiaulax hazeni: Latest Tiffanian (late Paleocene) of Wyoming (type locality [Jepsen 1940]).

Referred specimens: UALVP 34994, 34993, 34996, P4s; 35235, M1; 35249, 35250, 35251, M2s; 34988, 34991, 35232, 35233, p4s; 35236, 35243, 35244, 35245, 35246, 35247, m1s; 35252, m2.

Horizon: Hand Hills West, Upper Level and Lower Level.

Description and discussion:

The p4's are fragmentary. The number of serrations cannot be determined, but comparison was made on the basis of blade profile. The cups formula of m1 is 4:7, of m2 is 5:3, of P4 is 2-3:8-10, of M1 is 7:4, and of M2 is 3-4:3:1.

Krause (1977) described Neoplagiaulax sp., cf. N. hazeni from the late Tiffanian Roche Percée local fauna. The specimens from the Hand Hills West, Upper Level, and Lower Level are morphologically identical to homologous teeth referred to Neoplagiaulax sp., cf. N. hazeni by Krause (1977). This material has been adequately described and figured by Krause (1977). There are no significant differences between the samples from the Upper Level and the Lower Level.

Neoplagiaulax hunteri (Simpson 1936)

(Figure 10a, b; Table 6)

Holotype: AMNH 33865, right dentary with i1-m2.

Type locality: Scarritt Quarry, Melville Formation, eastern Crazy Mountain Basin, Sweetgrass County, Montana.

Known age and distribution: Earliest Tiffanian (late Paleocene) of Montana (Douglass Quarry, Melville Formation, eastern Crazy Mountain Basin, Sweetgrass County [Krause and Gingerich 1983]) and Alberta (Cochrane 2, Porcupine Hills Formation); early Tiffanian of Montana (type locality [Simpson 1936]); middle Tiffanian of North Dakota (Brisbane locality, Tongue River Formation, Williston Basin, Grant County [Holtzman 1978]), Wyoming (Cedar Point Quarry, Polecat Bench Formation, Bighorn Basin, Bighorn County [Rose 1981]) and Alberta (UADW-2 locality, Paskapoo Formation, Blindman River [Fox 1990], Birchwood locality, Paskapoo Formation, Drayton Valley (Webb In prep.); late Tiffanian of North Dakota (Judson locality, Tongue River Formation, Williston Basin, Morton County [Holtzman 1978), Saskatchewan (Roche Percée Local Fauna, Ravenscrag Formation [Krause 1978]) and Alberta (Police Point locality, Ravenscrag Formation, Cypress Hills [Krishtalka 1973], Swan Hills Local Fauna, Paskapoo Formation, Swan Hills [Stonley 1988]).

Referred specimens: UALVP 34992, P4; 35237, M1; 35248, 35254, M2s; 34985, 34984, p4s; 35241, 35242, m1s; 35253, m2.

Horizon: Hand Hills West, Upper Level and Lower Level.

Description and discussion:

The p4's are fragmentary. The number of serrations cannot be determined, but comparison was made on the basis of blade profile. The cusp formula of m1 is 4-5:10, of m2 is 5:3, of P4 is 2:8, of M1 is 5:10:8, and of M2 is 4:3:1.

The dentition of this species has been adequately described and figured by Krause (1977) and Krause and Gingerich (1983). There are no significant differences between the samples from the Upper Level and the Lower Level.

Neoplagiaulax sp.

(Figure 11a, b; Table 7)

Referred specimens: UALVP 35238, 35239, 35240, 35255, M1s; 34946, 34947, 34989, 35234, p4s.

Horizon: Hand Hills West Upper Level and Lower Level.

Description and discussion:

M1. - These specimens are morphologically similar to the M1 of N. hazeni (Jepsen 1940), and the M1 of Neoplagiaulax sp., cf. N. hazeni, from the late Tiffanian Roche Percée locality (see Krause 1977), but are shorter with fewer lingual cusps. There are fewer labial cusps (5-6:10-11:5-7) than the M1 of N. hunteri (Simpson 1936).

p4. - The lower fourth premolars have 14 to 15 serrations, with a high arcuate profile. The distance from the anterobasal concavity to the first serration is 2.25mm, less than 1/3 the total length of the blade. The posterior basal cuspule is crescent-shaped and located far posterior at the base of the blade.

These specimens are similar to the p4 of N. holtzmani n. sp. (undescribed material, UADW-2 locality, Blindman River) in having 15 serrations, a high arcuate profile, a straight posterior edge, and crescent-shaped posterior basal cuspule. It differs from N. holtzmani in having a longer and wider exodaenodont lobe, the highest serration is located further posteriorly, and stronger serrations are developed on the posterior part of the blade. The wider exodaenodont lobe is similar to that on the p4 of *N*. *pakapooensis* n. sp. (undescribed material, R.C. Fox, UADW-2 locality, Blindman River), but the distance between the anterobasal concavity and the first serration is longer in these specimens and there are more serrations than in the p4 of *N*. *paskapooensis*. The specimens are smaller than the p4 of *N*. *douglassi*, and similar in size to the p4 of *N*. *tenius* n. sp. (undescribed, UADW-2 locality, Blindman River), *N*. *hazeni* (Jepsen 1940), and *N*. *hunteri* (Simpson 1936). The posterior basal cuspule extends further anteriorly along the blade than in *N*. *tenius*, has a lower blade profile and convex posterior edge unlike the p4 in *N*. *hazeni*, and a flat rather than convex labial side of the blade, and smaller exodaenodont lobe than in *N*. *hunteri*. The anterobasal cuspule extends further anterior as in *N*. *jepi* (Rose 1981a).

Family Ptilodontidae Gregory and Simpson 1926

Ptilodus Cope 1881

Ptilodus sp. C (Krause 1987)

(Figure 12a-f; Table 8)

Holotype: UM 63094, right dentary fragment with i1, p3-p4.

Type locality: Cedar Point Quarry, Polecat Bench Formation, northern Bighorn Basin, Bighorn County, Wyoming.

Known age and distribution: Late Torrejonian of Wyoming (Swain Quarry, Fort Union Formation, Carbon County [Rigby 1980]); early Tiffanian of Alberta (Cochrane 2 locality, Porcupine Hills Formation, Cochrane [Youzwyshyn 1988]); middle Tiffanian of Wyoming (Cedar Point Quarry, Polecat Bench Formation, Bighorn Basin, Bighorn County [Krause 1987a]), North Dakota (Brisbane locality, Tongue River Formation, Grant County [Holtzman 1978]), Alberta (UADW-1, UADW-2, UADW-3 localities, Paskapoo Formation, Blindman River [Fox 1990], Birchwood locality, Paskapoo Formation, Drayton Valley [M.W. Webb, in prep.]); late Tiffanian of Saskatchewan (Roche Percée Local Fauna, Ravenscrag Formation [Krause 1982, 1987a]).

Referred specimens: UALVP 34976, 34977, P1s; 34978, 34979 P2s; 34980, P3; 34972, P4; 34973, 34974, 34982, m1s; 34975, m2.

Horizon: Hand Hills West, Upper Level.

Description:

The first and second upper premolars are of characteristic Ptilodus construction. P1 is triangular in occlusal outline, with two roots, and wrinkled enamel. P2 is rectangular in occlusal outline, with four crenulated cusps. There are strong vertical striations on the external surface of the cusps. These tooth positions have been adequately described and figured from the earliest Tiffanian Cochrane 2 locality (Youzwyshyn 1988), and the late Tiffanian Roche Percée (Krause 1977).

P3. - P3 is rectangular in outline with a posterolabial bulge. UALVP 34980 differs from the descriptions of the P3 of Ptilodus sp. C (Ptilodus "cedrus", see Krause 1982) in having a cusp formula of 3:2, rather than 3:3 (Krause 1977). P3s of Ptilodus sp. C from the middle Tiffanian Birchwood locality (see M.W. Webb in prep.) range in cusp morphology from 3:2 to 3:3. The overall dimensions and morphology support the inclusion of this specimen in this species.

P4. - The cusp formula of UALVP 34922 is 7:10. This specimen is larger than the p4 of the undescribed species P. "gnomus" (see Youzwyshyn 1988) and P. kummae, and smaller than the P4 of Ptilodus sp. T (Ptilodus "titanus", see Krause 1977), and similar to that of the Torrejonian species P. montanus (see Douglass 1908) in size. This specimen is morphologically identical to the descriptions for the p4 of Ptilodus sp. C from the late Torrejonian (see Rigby 1980) and middle Tiffanian (see Krause 1977). The p4 of Ptilodus sp. T differs from that of Ptilodus sp. C in being larger, with more cusps in the labial and lingual rows. The Hand Hills West specimens are intermediate in terms of size and cusp formula between the p4 of Ptilodus sp. T ((1-2)7-9:10-11:0, L=6.1mm, W=2.6mm) and Ptilodus sp. C ((2)6:9:0, L=5.8mm, W=2.7mm) from the Birchwood locality (see M.W. Webb in prep.). Teeth of Ptilodus sp. T have not been recovered from the Hand Hills West, Upper Level, but this is likely due to taphonomic bias. UALVP 34972 is tentatively referred to Ptilodus sp. C, based on the other material recovered from the Hand Hills West, Upper Level. The lower molars have been adequately described and figured by Krause (1977), and Gunnell (1994). The cusp formula of m1 is 7:6, and that of m2 is 4:2. Youzwyshyn (1988) noted that the m1 of this species possesses a greater number of cusps in all rows than does the m1 in other species of Ptilodus of similar size.

Discussion:

Krause (1982, Table 47, Figure 28) using the stratophenetic approach (Gingerich 1975, 1976) proposed the biostratigraphic zonation of North America, from the Paleocene to the Early Eocene, based on Ptilodus. Ptilodus sp. T (Ptilodus "titanus", see Krause 1982) occurred in the earliest Tiffanian, Ti1 (Plesiadapis praecursor Zone), and Ptilodus sp. C (Ptilodus "cedrus", see Krause 1982) occurred in the early Tiffanian, Ti2 (Plesiadapis anceps zone) and the middle Tiffanian, Ti3 (P. rex Zone).

Youzwyshyn (1988) described material of Ptilodus sp. C and Ptilodus sp. T from the earliest Tiffanian of Alberta, at the Cochrane 2 locality, indicating that these two species of Ptilodus were contemporaneous in the early Tiffanian. The above species have also been recovered from the middle Tiffanian Birchwood locality (M.W. Webb in prep.), UADW-2 locality (Fox 1990), and the Hand Hills West, Upper Level, indicating that they remained contemporaneous in the middle Tiffanian.

Ptilodus sp.

(Figure 12g,h)

Referred specimens: UALVP 34981, P4; 34983, m1.

Horizon: Hand Hills West, Upper Level.

Description:

P4. - The enamel of this specimen is absent from all but the occlusal surface, making the size difficult to determine. The estimated dimensions for this specimen are L=5.0mm, W=2.5mm. This is smaller than the p4 of Ptilodus sp. C (Krause 1987) and Ptilodus sp. T (Krause 1987) and larger than that of P. gnomus (new species in Youzwyshyn 1988) and P. kummae (Krause 1977). The cusp formula is 0:6-7?:9. The labial row of the cusp forumla is indicated as possessing six or seven cusps, as the anterior portion of the enamel, including the base of the cusps, is absent; and a small cusp may have been present. The cusps of the lingual row are all of uniform height and in line.

The absence of a third row of cusps is characteristic of the p4 of P. wyomingensis and P. montanus (Cope 1881, Krishtalka 1973). UALVP 34981 is similar to the p4 of P. wyomingensis (PU14468 L=5.2mm, W=2.4mm), from the late Torrejonian of Wyoming (Rock Bench Quarry, see Jepsen 1940) in terms of the size, shape, and number of cusps. The entire lingual row of cusps is oriented slightly lingually, rather than straight anteroposteriorly as in the p4 of P. wyomingensis. This specimen also bears a resemblance to material referred to P. montanus from the middle Tiffanian Joffre Bridge locality (pers. obs.).

m1. - The dimensions of this specimen are L=3.6mm, W=1.8mm. This is larger than the m1 in P. "gnommus" (new species in Youzwyshyn 1988) and P. kummae, but smaller than the m1 of Ptilodus sp. C (Krause 1987) and Ptilodus sp. T (Krause 1987). The cusp formula is 6:7. UALVP 34983 is within the size range of the m1 in P. montanus, P. wyomingensis and P. mediaevus, but possesses too many cusps (P. montanus, P. wyomingensis and P. mediaevus have fewer than six cusps in the labial row). It is similar in size and cusp formula to the m1 of Ptilodus sp., from the late Tiffanian of Alberta (Police Point, see Krishtalka 1973, Swan Hills, see Stonely 1988).

Discussion:

Rigby (1980) recovered material from the late Torrejonian Swain Quarry locality referrable to P. wyomingensis, P. montanus, and P. mediaevus (Cope 1881, Krause 1982). Based on the variation in blade profile of samples determined to be P. mediaevus, Rigby synonymized "P. ferronensis" from the Dragon locality with P. mediaevus, and suggested that P. wyomingensis and P. montanus are conspecific with P. mediaevus. The apparent differences are due to intraspecific variation in the separation of the anterior and posterior buttresses and the definition of the serrations (Rigby 1980).

Krause (1982) suggested that P. wyomingensis, P. montanus and P. mediaevus are separate and distinct species, P. mediaevus being high crowned, P. wyomingensis being low crowned and smaller than P. montanus.

The specimens from the Hand Hills West, Upper Level, are similar in terms of morphology to homologous teeth of P. wyomingensis, P. montanus, and P. mediaevus. The features present and the worn condition of the P4 preclude identification to the species level, and do not provide information as to the relationships of these species.

Genus Prochetodon Jepson 1940

Prochetodon sp., cf. P. foxi Krause 1987

(Figure 13)

Holotype of Prochetodon foxi: YPM-PU 21223, right dentary with base of I1 and P3-4.

Type locality: Long Draw Quarry, Bighorn Basin, Carbon County, Montana.

Known age and distribution of Prochetodon foxi: Middle Tiffanian (Ti3) of Alberta (Birchwood locality, Paskapoo Formation [M.W. Webb in prep.]); and late middle Tiffanian (Ti4) of North Dakota (Judson Locality, Tongue River Formation, Williston Basin, Morton County [Holtzman 1978]), Alberta (Swan Hills site 1, Paskapoo Formation [Russell 1967, Stonely 1988]), Saskatchewan (Roche Percée Local Fauna, Williston Basin [Krause 1977]), Montana (type locality, Bighorn Basin [Jepsen 1940, Krause 1987b]), and Wyoming (Divide Quarry, Bighorn Basin [Gingerich 1976a], Malcolm's locality, Wind River Basin [Krishtalka et al. 1975]).

Referred specimen: UALVP 34987, p4.

Horizon: Hand Hills West, Upper Level.

Description and discussion:

UALVP 34987 has 16 serrations (L=9.1mm, W=3.1mm, H=6.0mm) and a small posterior basal cuspule that extends anteriorly, and terminates in line with the second furthest posterior serration. The crown is lower than the p4 in Ptilodus and has a smaller exodaenodont lobe, characteristic of the genus Prochetodon (Krause 1982, 1987a). The p4 of Prochetodon foxi has a lower profile with more serrations and is slightly larger than that of P. cavus (Jepsen 1940, Krause 1987b). UALVP 34987 specimen has more serrations, and is slightly larger than the p4 of Prochetodon foxi, from the late Tiffanian of Montana (Long Draw, Krause 1987b), and Saskatchewan (Roche Percée, Krause 1987b) and the middle Tiffanian of Alberta (UADW-2 locality, Fox 1990, Birchwood locality, M.W. Webb in prep.).

Genus *Baiotomeus* Krause 1987

Baiotomeus sp.

(Figure 14)

Referred specimens: UALVP 34954, 34955 P4's.

Horizon: Hand Hills West, Upper Level.

Description:

Cusp formula 4:4-7:8. UALVP 34954 possesses seven cusps in the medial row. The fifth, sixth and seventh cusp are located labially and are closely appressed. The posterior basal depression is well developed, and bordered by a crest labially and a small cuspule lingually.

These specimens are (L=2.2mm, W=1.0mm) within the size range of the P4 in *B*. *russelli* (Youzwyshyn 1988). *B*. *russelli* is the smallest species of *Baiotomeus*, approximately 45% smaller than those of *B*. *douglassi* (Simpson 1935a, Krause 1987b), and 40% smaller than those of *B*. *lamberti* (Krause 1987b). The specimens from the Hand Hills West, Upper Level, are morphologically similar to homologous teeth referred to *Baiotomeus* *russelli* from the earliest Tiffanian Cochrane 2 locality, but they differ slightly in cusp formula, ((3-4):5:8:0, see Youzwyhsyn 1988). These specimens are referred to *Baiotomeus* sp. until further comparative material is recovered from the Hand Hills West, Upper Level, or other middle Tiffanian localities.

Discussion:

The genus Baiotomeus was previously recorded from the Torrejonian and the earliest Tiffanian of Montana (Simpson 1935a, Krause 1987b). Youzwyshyn (1988) extended its geographical distribution in the earliest Tiffanian to Alberta. The recovery of Baiotomeus from the Hand Hills West, Upper Level, extends the geological time range of this genus to the middle Tiffanian (Table 31).

Subclass Theria Parker and Haswell 1880

Infraclass Metatheria (Huxley 1880)

Superorder Marsupialia (Illiger 1811)

Order Marsupicarnivora Ride 1964

Family Didelphidae Gray 1821

Subfamily Didelphinae (Gray 1821)

Tribe Peradectini Crochet 1979

Genus Peradectes Matthew and Granger 1921

Peradectes elegans Matthew and Granger 1921

(Figure 15a-c; Table 9)

Holotype: AMNH 17376, paired dentaries with rp1, p3-m4 and lp2-m4.

Type locality: Mason Pocket, Animas Formation, San Juan Basin, Colorado (Lucas and Ingersoll 1981).

Known age and distribution: Middle Tiffanian of Wyoming (Cedar Point Quarry, Polecat Bench Formation, Fort Union Formation, Bighorn Basin, Bighorn County [Krishtalka and Stucky 1983]), Colorado (Type locality [Lucas and Ingersoll 1981]), North Dakota (Brisbane locality, Tongue River Formation, Grant County [Holtzman 1978]), and Alberta (UADW-2 locality, Paskapoo Formation, Blindman River [Fox 1983, 1990], Joffre Bridge, Paskapoo Formation, Red Deer River [Fox 1990]); early Wasatchian of Wyoming (Four Mile Area, Wasatch Formation [Krishtalka and Stucky 1983]).

Referred specimens: UALVP 34903, M1; 34904, 34905, M3s; 34900, 34901, m1s; 34925, m2s; 34902, m3.

Horizon: Hand Hills West, Upper Level.

Description and discussion:

M1. - The lingual part of the tooth is narrow, resembling an equilateral triangle in occlusal view (Simpson 1935a). The protoconid is shifted anteriorly, unlike the more buccal position in M2, as noted by Krishtalka and Stucky (1983). All stylar cusps with the exception of cusp A (parastyle) are present, with cusps B (stylocone) and D being well developed. Cusp E (metastyle) is set off from the rest of the stylar cusps by a small shallow basin. The precingulum is well developed, shelf-like, and extends virtually the entire anterior surface.

M3. - The M3 is more transversely narrow than M1 and M2, with an anteroposteriorly compressed protocone and protoconal basin. The metacone leans posteriorly, and the postmetacrista is well developed. The stylar shelf and cusps are present and developed as in M1, but with a deeper ectoflexus. This tooth is comparable in size to those samples from the middle Tiffanian UADW-2 locality (see Fox 1983) (L=2.1mm, W=1.8mm), and slightly larger than those published for the middle Tiffanian Cedar Point Quarry (see Krishtalka and Stucky 1983). This specimen differs from the M3 of Peradectes sp. recovered from the earliest Tiffanian Cochrane 2 locality (see Youzwyshyn 1988) in being smaller and more transversely narrow.

m1. - The lower first molars are represented by two isolated specimens. The cusps are high and distinctly conical in shape. The protoconid is the highest trigonid cusp, the metaconid is intermediate in size, and the paraconid is small and leans anterolingually. The talonid is deeply basined, and is considerably lower than the trigonid with the entoconid being the highest talonid cusp. These specimens are morphologically identical to homologous teeth referred to Peradectes elegans by Krishtalka and Stucky (1983) from the middle Tiffanian of Wyoming and UALVP 16270 recovered from the middle Tiffanian UADW-2 locality of Alberta (see Fox 1983). The Hand Hills West, Upper Level, molars differ from the UADW-2 material in the pre- and postcingulid being better developed, almost shelf-like in appearance.

m2. - The talonid of this single isolated tooth is wider than the trigonid, unlike m1, but less so than in m3. The precingulid is relatively well developed, and the paraconid is inclined directly anteriorly rather than anterolingually as in m1. The cristid obliqua appears to be slightly more lingual, than in m3, forming a more narrow hypoflexid notch. This tooth is smaller than the samples from the middle Tiffanian Bison Basin (see Krishtalka and Stucky 1983), San Juan Basin of New Mexico (see Lucas and Ingersoll 1981) and the early Wasatchian Four Mile Area (see Krishtalka and Stucky 1983).

m3. - Overall, this tooth is larger than m1 and m2, transversely wider relative to its length, giving a more squared appearance in occlusal view. The talonid is distinctly wider than the trigonid, characteristic of m3 in Peradectes (see Krishtalka and Stucky 1983). The protoconid remains the highest trigonid cusp, the paraconid is more medially located than on m1 and m2, the hypoconulid is erect, not sloped posterolingually as in m1 and m2, and the cingula are vestigial.

Peradectes sp.

(Figure 16a,b; Table 10)

Referred specimens: UALVP 34906, M3; 34926, m2.

Horizon: Hand Hills West, Upper Level.

Description:

M3. - This upper third molar is significantly smaller than the specimen from the Upper Level referred to Peradectes elegans, has a more lingually compressed protocone, and narrower stylar shelf. This specimen shares some features with the M3 of P. elegans, including a relatively shallow ectoflexus, and a more narrow protoconal base. Like in the M3 of P. pauli, from the Bison Basin of Wyoming, the protocone is anteroposteriorly compressed, and the paracone and metacone are set further apart than in P. elegans, with a straight centrocrista. Overall this specimen is more transversely wide than P. elegans, although not as wide as the published material for P. pauli (see Krishtalka and Stucky 1983). Despite the heavily worn stylar shelf, UALVP 34926 appears that cusp B (stylocone) and cusp D were the highest stylar cusps, and are subequal in height.

m2. - The lower second molar is characterized by tall, sharp conical cusps, with a closely twinned entoconid and hypoconulid, as is characteristic of Peradectes (see Krishtalka and Stucky 1983). It is significantly smaller than the m2 of P. elegans, and within the range given for P. pauli (L=1.2mm, W=0.8mm) (see Krishtalka and Stucky

1983). The cusps of this specimen are extremely worn, making identification difficult. Further samples are necessary to clarify the taxon that this specimen represents.

Discussion:

These specimens closely resemble homologous teeth of P. pauli in terms of size and cusp development. However, the protoconal base of the M3 is more narrow, which has been suggested to be a derived feature seen in P. elegans and later species of Peradectes (see Krishtalka and Stucky 1983). These specimens may indicate that the distribution of P. pauli, previously known only from the Bison Basin of Wyoming, extended into more northerly regions during the middle Tiffanian, as in P. elegans. The M3 may represent an individual variant of P. pauli, a subspecific difference reflecting the extended geographic distribution, or a different species, more primitive than P. elegans, and possibly more closely related to P. pauli, but slightly more derived. These specimens are referred to Peradectes sp. until futher comparative material is recovered.

Infraclass Eutheria Gill 1872

Order Primates Linnaeus 1758

Suborder Plesiadapiformes Simons and Tattersal in Simons 1972

Superfamily Plesiadapoidea Trouessart 1897

Family Saxonellidae Russell 1964

Genus Saxonella

Saxonella naylori Fox 1984

(Plate 1A)

Holotype: UALVP 16201, an incomplete left dentary having i1, p3-p4, m1.

Type locality: UADW-2 locality, Paskapoo Formation, Blindman River.

Known age and distribution: Middle Tiffanian (late Paleocene) of Alberta (type locality [Fox 1984a, 1991], Hand Hills West, Upper Level, Paskapoo Formation [Fox 1991]).

Referred specimens: UALVP 29358, incomplete right dentary with p4, m1-m2; 34889, m2.

Horizon: Hand Hills West, Upper Level.

Description:

m2. - UALVP 34889 (L=1.6mm, AW=1.1mm, PW=1.5mm) represents a relatively complete lower second molar. The features of this specimen are: (1) the protoconid although absent from this specimen, appears to have had a larger base than the metaconid; (2) the metaconid is prominent; (3) the paraconid is reduced and is situated slightly more labially than the metaconid; (4) the talonid is well developed and deeply basined; (5) the entoconid is the highest talonid cusp and conical; (6) the hypoconid is smaller with a slightly wider base; (7) the entocristid is distinct and straight; and (8) the postcristid is well developed and continuous along the labial side of the tooth past the hypoconid.

UALVP 29359 was previously described and figured by Fox (1991).

Discussion:

Saxonella naylori is known from the middle Tiffanian of Alberta from localities along the Blindman River and the Hand Hills West, Upper Level (see Fox 1984a, 1991). Fox (1991) noted that the molars of the Hand Hills West specimen (UALVP 29358) differed from the Blindman River material in being slightly larger, with the p4 being smaller and having a well developed paraconid (see Fox 1991). This specimen was referred to S. naylori, based on the primitive condition of the p4 (see Fox 1991). In addition to these features, the lower molars of the Hand Hills West, Upper Level, differ from the holotype of S. naylori from UADW-2 in being slightly larger, comparable in size to the European species S. crepature, and the trigonid is wider and appears more squared in occlusal view, rather than anteriorly tapered as in S. naylori from the Blindman River localities. The m2 of Saxonella crepature is not known. The Hand Hills West specimens may represent intraspecific or geographical variation in S. naylori, or a different species than the one recovered from UADW-2, more similar to the European species. Further samples are required to confirm that these represent a separate species rather than individual variation.

An isolated m2 from the middle Tiffanian Birchwood locality was referred to Saxonellidae indeterminate genus and species (M.W. Webb in prep.). The m2 differs from *Saxonella naylori* in being wider relative to its length. The Hand Hills West specimen is similar in terms of morphology, but is much smaller.

Family Carpolestidae Simpson 1935

Genus Elphidotarsius Gidley 1923

Elphidotarsius wightoni Fox 1984

(Figure 17a, b; Plate 1B; Table 11)

Holotype: UALVP 21001, incomplete left dentary having incisor, p4, m1-m3, and having two small postincisor teeth and an alveolus anterior to p4.

Type locality: UADW-1, UADW-2 localities, Paskapoo Formation, Blindman River.

Known age and distribution: Early Tiffanian (late Paleocene) of Alberta (Hand Hills West, Lower Level, Paskapoo Formation [Fox 1990]); middle Tiffanian of Alberta (type locality, [Fox 1984b], Hand Hills West, Upper Level, Paskapoo Formation [Fox 1990], Birchwood locality, Paskapoo Formation, Drayton Valley [M.W. Webb in prep.]).

Referred specimens: UALVP 35146, left maxillary fragment with M1-M3; 34862, P4; 34863, M3; 34864, 34873, m2s; 34998, i1; 34857, 34865, 34857, p4s; 34940, 34851, 34866, m3s.

Horizon: Hand Hills West, Upper Level and Lower Level.

Description:

P4. - UALVP 34862 represents the highly modified carpolestid upper fourth premolar, with four buccal cusps. The fourth, and furthest posterior, is the highest cusp.

The median row consists of a centrally located cuspule, with cuspate cristae. The protocone and protoconule basin is missing from this specimen, so I am unable to determine if the hypocone is not placed as far lingually as in other species of Elphidotarsius (see Rose 1981), as is characteristic of E. wightoni (Fox 1984b). It is more triangular than squared in occlusal view, also characteristic of E. wightoni (Fox 1984b).

M1 -M3 are morphologically identical to UALVP 21007 from the type locality (UADW-2, Blindman River) for E. wightoni (Fox 1984b). The upper molars of E. wightoni have been adequately described and figured by Fox (1984b).

i1. - UALVP 34998 is a moderately worn right lower first incisor. This tooth position has been adequately described and figured by Fox (1984b).

p4. - These teeth are the characteristically modified plagiaucoid lower fourth premolar of carpolestids, with four apical cusps, as in Elphidotarsius (see Rose 1981). The second apical cusp is the highest, the third situated slightly labially, and the talonid is reduced, as in of E. wightoni (Fox 1984b). In E. russelli, the third apical cusp is the highest, and the apical cusps are in line (Krause 1978, Rose 1975). In E. shotgunensis, the metaconid is situated far to the lingual side (see Rose 1975).

m2. - The cusps are high and conical. The metaconid is the highest trigonid cusp, the entoconid is the highest talonid cusp, and the ectocingulum is well developed. These specimens are distinctly smaller than the m2 of E. russelli and E. shotgunensis, and slightly smaller than that of E. florencae (see Rose 1975). The talonid is completely squared, unlike that in E. russelli, in which the talonid is elongated more anteroposteriorly.

These specimens are morphologically identical to the m2 on the holotype from the Blindman River (UALVP 21001, Fox 1984b).

m3. - The metaconid is the highest trigonid cusp and leans posteriorly, the protoconid is low, and the paraconid is in line with the metaconid. The hypoconulid lobe is well developed and shifted slightly lingually, with the entoconid being the highest cusp. The talonid is open and sloped slightly labially, and the precingulid is reduced. The talonid of UALVP 34940 is moderately worn giving the labial side of the basin a sharply inclined appearance. UALVP 34851 is not as worn and is slightly larger than UALVP 34940, UALVP 34866 and the type specimen (UALVP 21001), but not within the range of E. russelli (Krause 1978).

Discussion:

There is no significant difference between the samples from the Upper Level and the Lower Level.

Elphidotarsius sp.

(Figure 18c)

Referred specimen: UALVP 34867, m2.

Horizon: Hand Hills West, Lower Level.

Description:

UALVP 34867 is an isolated right lower second molar. The features of this specimen are: (1) high, sharp cusps; (2) squared in occlusal view; (3) distinctively squared talonid; (4) the paraconid is small and cuspate; (5) the metaconid is the highest trigonid cusp and is slanted slightly posteriorly; (6) the protoconid is low and located slightly posterior to the metaconid; (7) the entoconid and hypoconid are subequal in size; and (8) the cingula are weakly developed.

Discussion:

The poorly developed cingula represent a primitive feature, and the high, sharp cusps represent a derived one (Fox 1984b). In terms of size (L=1.0mm, W=1.0mm), this specimen is smaller than E. russelli (see Rose 1975), and within the range of E. wightoni (Fox 1984b)). The lower second molar of E. shotgunensis is not known, although this specimen is likely too small to be referrable to that species. The overall size, the prominence of the metaconid and the squared talonid are consistent with E. florencae

(Rose 1975). In E. russelli, the metaconid and paraconid are subequal. However, the high cusps and squared talonid suggest an affinity with E. wightoni, (Fox 1984b). The reduced cingulum and distinct hypoconid may represent individual variation within E. wightoni.

Elphidotarsius russelli Krause 1978

(Figure 18a, b; Table 12)

Holotype: UALVP 11742, left p4.

Type locality: Cochrane site 2, Porcupine Hills Formation, southwestern Alberta.

Known age and distribution: Earliest Tiffanian (late Paleocene) of Alberta (type locality [Krause 1978, Youzwyshyn 1988]); and early Tiffanian of Alberta (Hand Hills West locality, Lower Level, Paskapoo Formation, Hand Hills [Fox 1990]).

Referred specimens: UALVP 34868, I1; 34861, P3.

Horizon: Hand Hills West, Lower Level.

Description:

I1. - The features of UALVP 34868 are as follows: (1) the anterocone (the top portion is broken) and laterocone are well developed; (2) the posterocone is distinct; (3) the posterocrista forms a shelf-like extension; (4) a basomesial cuspule is present but worn; and (5) a mediocone is lacking which increases the width of the occlusal surface. The absence of a basomesial cuspule is characteristic of the I1 of Elphidotarsius wightoni (Fox 1984b) and Carpodaptes hazelae (see Rose 1975). The absence of a mediocone is characteristic of C. hazelae. This specimen is morphologically identical to homologous teeth referred to E. russelli from the type locality (UALVP 18619, see Youzwyshyn 1988).

P3. - UALVP 34861 represents the highly modified carpolestid upper third premolar, with three buccal cusps. There is a high buccal ridge connecting the posterior two cusps through most of their height. The second cusp is the highest, and there is a well-developed hypocone and precingulum. The first, anterior most cusp is low and offset from the other cusps. The paraconule is distinct, as is the preparaconule crista, which is characteristic of the P3 of E. russelli (see Rose 1975). The protocone and basin are wide and provide a more squared occlusal view, unlike the P3 of E. wightoni, which is more narrow and appears more triangular in occlusal view (Fox 1984b).

Discussion:

The morphology of the P3 is consistent with the position of E. russelli as intermediate between E. wightoni and Carpodaptes hazelae (see Fox 1984b). The more triangular appearance of P3 in E. wightoni represents the primitive condition, whereas the more squared shape is characteristic of the more derived condition in C. hazelae. The upper incisor also supports this view. The occlusal surface of the I1 is wider than in E. wightoni, yet more narrow than in C. hazelae.

The recovery of Elphidotarsius russelli, E. wightoni and Carpodaptes sp., cf. C. hazelae from Hand Hills West, Lower Level, indicates that they were contemporaneous during the early Tiffanian. It extends the geological time range of E. wightoni, to the early Tiffanian (Table 31). Previously E. russelli was known from the earliest Tiffanian (Ti1) and the early Tiffanian (Ti2), and E. wightoni had only been recovered from middle Tiffanian localities (Ti3). Fox (1984b) argued that E. wightoni represents a more primitive species of Elphidotarsius and one more closely related to the ancestry of Carpodaptes than E. russelli and the other species of Elphidotarsius, although itself not ancestral to Carpodaptes. Therefore, one would expect to find it in horizons that produce geologically older species of Elphidotarsius.

Genus Carpodaptes Matthew and Granger 1921

Carpodaptes hazelae Simpson 1936

(Figure 19; Table 13)

Holotype: AMNH 33854, right dentary fragment with p4-m3.

Type locality: Scarritt Quarry, Melville Formation, eastern Crazy Mountain Basin, Sweetgrass County, Montana.

Known age and distribution: Earliest Tiffanian (late Paleocene) of Wyoming (Keefer Hill locality ["Shotgun local fauna"], Fort Union Formation, Wind River Basin, Fremont County) [Gazin 1956]); early Tiffanian of Montana (type locality [Simpson 1936, Rose 1975]), and Alberta (Cochrane 2, Porcupine Hills Formation [Youzwyshyn 1988]), middle Tiffanian of Wyoming (Cedar Point Quarry, Polecat Bench Formation, Bighorn Basin, Bighorn County [Rose 1975, 1981]) and Alberta (UADW-1, UADW-2, UADW-3 localities, Mel's Place, Paskapoo Formation, Blindman River [Fox 1984b, 1990], Joffre Bridge Roadcut locality, lower level, Paskapoo Formation, Red Deer River [Fox 1990], Hand Hills West locality, Upper Level, Paskapoo Formation, Hand Hills [Fox 1990], Birchwood locality, Paskapoo Formation, Drayton Valley [M.W. Webb in prep.]).

Referred specimens: UALVP 34854, P3; 34853, M2; 34847, 34848, 34849, p4s; 34855, 34850, m2s; 34852, m3.

Horizon: Hand Hills West, Upper Level.

Description:

The dentition of *Carpodaptes hazelae* has been adequately described and figured by Simpson (1936) and Krause (1978). The p4s, m2s, m3, and P3 are further described as these tooth positions are variable, and differ between the Upper Level and Lower Level.

P3. - UALVP 34854 represents an upper third premolar, with four stylar cusps connected through most of their height by a buccal ridge. The second stylar cusp is the highest, the two anterior most cusps are inclined posteriorly, and the third is inclined anteriorly. The hypocone is well developed and in line with the protocone. p4. - The lower fourth premolars are characterized by: (1) five apical cusps in line; (2) the fifth cusp is small and offset from the others; (3) the second cusp is the highest; (4) the talonid is relatively well developed, with distinct cusps, and sloped slightly posteriorly; and (5) there is a small lingual depression between the first apical cusp and the talonid. These specimens are morphologically identical to homologous teeth from the middle Tiffanian UADW-2 locality (pers. obs.). This tooth position of *Carpodaptes hazelae* has been adequately described and figured by Rose (1975) and Krause (1978).

m2. - The features of the lower second molars are: (1) the metaconid is the highest trigonid cusp; (2) the paraconid is distinct and offset slightly labially relative to the metaconid; (3) the hypoconid and entoconid are subequal in height; (4) the trigonid and talonid are deeply basined; and (5) the cingula are distinct giving a squared appearance in occlusal view. These specimens are morphologically similar to material from the late

Tiffanian Roche Percée locality (see Krause 1978), but the trigonid is slightly anteroposteriorly compressed relative to the talonid.

m3. - As in m2, the metaconid is the highest trigonid cusp, and the paraconid is distinct and in line with the protoconid. The hypoconulid lobe is well developed and medially located, the entoconid and hypoconid are distinctly lobed, and the entocristid is cuspate.

Discussion:

Krause (1978) described two different morphs of C. hazelae from the early Tiffanian Scarritt Quarry of Montana, and the middle Tiffanian Cedar Point Quarry of Wyoming. The p4s from the Hand Hills West, Upper Level, resemble the Scarritt Quarry specimens in being slightly smaller, narrower, with a small lingual depression between the first apical cusp and the talonid.

Although, biostratigraphy based on carpolestids is not considered to be as useful as that based on plesiadapids, the presence of C. hazelae supports the conclusion that the Upper Level is middle Tiffanian in age (Rose 1975, Krause 1978).

Carpodaptes sp., cf. C. hazelae

(Figure 20)

Referred specimen: UALVP 34869, LDP4.

Horizon: Hand Hills West, Upper Level.

Description and discussion:

The features of this specimen are: (1) there are three labial cusps, the anterior two are appressed, and the third is separated; (2) the tips of the cusps are missing, but the first and third cusps appear to be the highest; (3) there are three cusps in the middle row; (4) the trigon is reduced, with a small protocone; and (5) the cristae are worn but appear to have been relatively well developed.

UALVP 34869 (L=2.1mm, W=2.1mm) likely represents a deciduous P3 or P4 of Carpodaptes hazelae. The central cuspule of the middle row is shifted anteriorly, as in P3, rather than being centrally located as in P4, but there are fewer labial cusps, as in P4. This specimen is tentatively identified as a DP4, based on its similarity in terms of size and morphology to the P4 of Carpodaptes hazelae.

Carpodaptes sp., cf. C. hazelae Krause 1978

(Figure 21a-e; Plate 1C, D; Table 14)

Referred specimens: UALVP 34858, right maxillary fragment with P4-M1; 35189, P3; 34856, 34859, P4s; 35259, M1; 34872, M3; 34860, lower left dentary fragment with p4-m3; 35272, left anterior dentary fragment with canine, and alveoli with roots of i1, i2, and the alveolus of p4; 35199, 35200, p4; 34997, m1; 34898, 34871, 35191, 34870, m2s.

Horizon: Hand Hills West, Lower Level.

Description:

The dentition of Carpodaptes sp., cf. C. hazelae from the late Tiffanian Roche Percée locality has been adequately described and figured (see Krause 1978). The following tooth positions are further described, P3, P4, p4, and canine.

P3. - The salient features of UALVP 35189 are: (1) four apical cusps; (2) the basin between the buccal cusps and the median row is deep; (3) the buccal cusps are connected through most of their height by a crest, with the anterior most cusp separated by a small depression; (4) the median cusp is well developed and in line with the protocone; (5) the hypocone is prominent.

P4. - Rose (1975) discussed the range of variation in size and shape of the P4s of within Carpodaptes hazelae. The specimens from the Hand Hills West, Lower Level demonstrate this variation. UALVP 34858 (Figure 21b) is larger than the P4s recovered from the middle Tiffanian UADW-2 locality (pers. obs.). It is similar in morphology to the early Tiffanian Scarritt Quarry specimen (AMNH 33980) in having a sixth incipient buccal cusp, but is wider. UALVP 34856 (Figure 21e) is more similar in morphology to the Scarritt Quarry specimen (AMNH 33981), but differs from UALVP 34858 in being narrower with no indication of a sixth cusp, and the width between the median crest and the buccal cusps is greater. Overall, these specimens represents an intermediate range in size and shape for C. hazelae. Teeth at this position have not been recovered from the Hand Hills West, Upper Level.

The P3, P4s, and upper and lower molars are morphologically identical to homologous teeth referred to Carpodaptes sp., cf. C. hazelae from the late Tiffanian Roche Percée Local Fauna (see Krause 1978).

p4. - These specimens have five apical cusps, the second cusp is the highest, the fifth cusp leans anteriorly. The p4s of Carpodaptes hazelae from the Hand Hills West, Upper Level, are narrow with high crowns as in the early Tiffanian Scarritt Quarry material (see Krause 1978). The p4s from the Hand Hills West, Lower Level differ from these in being shorter and smaller, morphologically identical to the p4's referred to Carpodaptes sp., cf. C. hazelae from the late Tiffanian Roche Percée Local Fauna by Krause (1978).

UALVP 35272 (Figure 21) is a left dentary fragment with canine, alveoli and roots of i1, i2, and the alveolus of p4. The alveolus of p4, posterior to the canine, is rounded, the root of i1 is larger than that of i2, laterally compressed and inclined anteriorly, the root of i2 is rounded and slanted anteriorly. The canine of C. hazelae, as far as I can determine, has not yet been recovered and described. The canine (L=1.1mm, W=0.6mm) is larger than that of Elphidotarsius wightoni (L=0.6-0.65mm, W=0.45mm, Fox 1984b), and more elongated, extending further anteriorly, similar to the condition seen in Carpodaptes cygneus (Rose 1981a). Based on its morphology and the recovery of Carpodaptes sp., cf. C. hazelae from the Lower Level, this specimen is referred to C. sp., cf. C. hazelae.

Discussion:

There are subtle differences between the samples from the Hand Hills West, Upper Level, and the Lower Level. The m2 and m3 are slightly smaller, and the p4 is shorter and more narrow than the material from the Upper Level. The significance of these differences is not known.

Family Plesiadapidae Trouessart 1897

Genus Plesiadapis Gervais 1877

Plesiadapis rex (Gidley 1923)

(Figure 22a-b; Table 15)

Holotype: USNM 9828, lm2.

Type locality: Locality 13, Sweetgrass County, Crazy Mountain Field, Montana.

Known age and distribution: Middle Tiffanian of Montana (type locality [Gidley 1923], Cedar Point locality, Polecat Bench Formation, Bighorn Basin, Bighorn County [Gingerich 1976b]), Wyoming (Hoback Basin, Battle Mountain Locality [Gingerich 1976b]), North Dakota (Brisbane locality, Tongue River Formation, Grant County [Holtzman 1978]), and Alberta (Erickson's Landing, UADW-2, Paskapoo Formation, Blindman River [Simpson 1927a, Fox 1990], Birchwood locality, Paskapoo Formation [M.W. Webb in prep.]).

Referred specimens: UALVP 34876, 34887, 34907, P4s; 34875, p4; 34874, m2.

Horizon: Hand Hills West, Upper Level.

Description:

These specimens do not differ significantly from the descriptions of Plesiadapis rex by Gidley (1923), Gazin (1956), Russell (1964), and Gingerich (1976b). The p4 and P4 differ from the middle Tiffanian Cedar Point Quarry material in being smaller and more narrow (see Gingerich 1976), and are further described here.

P4. - The features of these specimens are: (1) prominent paracone, larger than the metacone; (2) the paracone and metacone are joined through most of their height by a crest; (3) the paracone, paraconule, and protocone are in line; (4) well-developed conules; and (5) the preparacrista and postmetacrista are prominent and form a shallow basin. Plesiadapis rex differs from the early Tiffanian P. anceps in having a distinct metacone, and from the earliest Tiffanian P. praecursor in having prominent cingula.

p4. - UALVP 34875 is a right lower fourth premolar of Plesiadapis rex, characterized by a single trigonid cusp. The protoconid tends to be more inflated rather than wedge-shaped, as in the early Tiffanian P. anceps, but not as inflated as in the late Tiffanian P. churchilli (see Gingerich 1976). The talonid has two well-developed cusps, giving the talonid a squared appearance.

Discussion:

The biostratigraphic zonation of the late Paleocene is based on the lineage of Plesiadapis (Gingerich 1976, Archibald et al. 1987). The recovery of Plesiadapis rex from the Hand Hills West, Upper Level, indicates an age of middle Tiffanian (Ti3).

Genus Plesiadapis Gervais 1877

Plesiadapis sp., cf. P. rex (Gidley 1923)

(Figure 23)

Referred specimen: UALVP 34888, P3.

Horizon: Hand Hills West, Upper Level.

Description and discussion:

UALVP 34888 is more narrow than specimens referred to P4 of Plesiadapis rex from the Upper Level (L=1.6mm, W=2.4mm), but slightly larger than the P3 of Plesiadapis rex recovered from the middle Tiffanian UADW-2 locality (pers. obs.). This specimen is very worn, and the enamel is missing, obscuring other diagnostic features. The following features can be distinguished: (1) the paracone is larger than the metacone; (2) they are connected through most of their height; (3) the paraconule is well developed; and (4) the protocone is large and is in line with the paracone and paraconule. Based on the morphology of this specimen and the other plesiadapid material recovered from this horizon, this specimen is likely a P3 of P. rex.

Family Plesiadapidae Trouessart 1897

Indeterminate genus and species

Referred specimen: UALVP 34910, LM2.

Horizon: Hand Hills West, Lower Level.

Description:

UALVP 34910 is an extremely worn plesiadapid upper second molar, with the enamel completely absent. The following features can be distinguished: (1) squared in occlusal view; (2) hypocone distinct; (3) protocone shifted far anterior to be in line with the paracone; (4) reduced ectocingulum; (5) cristae likely well-developed, as they remain distinct despite the worn condition; and (6) conules are present, although may have been reduced.

Discussion:

The overall dimensions of this specimen (L=3.0mm, W=2.1mm) suggest that it was a moderately sized member of the genus Plesiadapis or a large species of Nannodectes. It appears to be too small, even if the enamel were present, to be referrable to Plesiadapis rex, but may be within the range for P. anceps, P. praecursor, or Nannodectes gazini, but it seems to be more narrow transversely than N. gazini (Gingerich 1976b). Size of teeth is a critical factor in species recognition, and as reliable measurements cannot be obtained for this specimen, any speculations as to its relationship below the family level would be uninformative.

Genus Nannodectes Gingerich 1975

Nannodectes simpsoni (Gazin 1956)

(Figure 24a-f; Table 16)

Holotype: USNM 20754, a right dentary with alveloi for i1, c1, p2-p3, crown of p4 and m1-m3 intact.

Type locality: Ledge locality, Bison Basin, Wyoming.

Known age and distribution: Late Paleocene (Tiffanian) of Wyoming (type locality [Gazin 1956a, Gingerich 1976]), Alberta (Swan Hills site 1, Paskapoo Formation, Swan Hills [Stonley 1988]), and Saskatchewan (Roche Percée Local Fauna, Ravenscrag Formation [Krause 1978]).

Referred specimens: UALVP 34880, M2; 34881, M3; 34879, p3; 34883, 34877, 34878, p4s; 34884, i1s.

Horizon: Hand Hills West, Upper Level

Description:

M2. - UALVP 34880 is a right upper second molar. The enamel is quite worn, but all the cusps and cuspules appear to have been well developed. The precingulum is distinct, there is no metastyle, and there is a small mesostyle. The paracone and metacone are separated by a small basin, and the centrocrista is straight. UALVP 34881 is a left upper third molar. In addition to the features mentioned previously, it is smaller than the m3 of N. gidleyi. The upper dentition of N. simpsoni has been adequately described and figured by Gazin (1956a) and Gingerich (1976b). The upper molars of Nannodectes simpsoni are more narrow than those of N. gidleyi (Gazin 1956a, Gingerich 1976b), larger than those of N. gazini (Matthew 1917, Gingerich 1976b), and not as squared in occlusal view.

i1. - The lower first incisors are characterized by a prominent medicone, and relatively well-developed margocristid and margoconid. They are narrower than the m1 of Plesiadapis and N. gidleyi. The well-developed mediocone represents the primitive condition; in later species, this is reduced to a ridge of enamel (see Gingerich 1976), like that seen in N. gidleyi. The lower first incisors have not been recovered for N. simpsoni. These specimens are tentatively referred to Nannodectes simpsoni, based on size and morphology.

p3. - The lower third premolar of Nannodectes is narrower, higher, and smaller than in members of the genus Plesiadapis. The protoconid is wedge-shaped and narrow, not as inflated as in p4, and the talonid is small with a single cusp centrally located. The talonid is not as squared as in N. gidleyi.

p4. - The lower fourth premolars are wedge-shaped, there is no paraconid or metaconid, and the talonid is moderately sized with two cusps. This specimen is morphologically identical to USNM 20754, referred to Nannodectes simpsoni (see Gingerich 1976).

Discussion:

The recovery of Nannodectes simpsoni from the Hand Hills region extends the geographic distribution from northwestern Alberta to southwestern Alberta.

Nannodectes gidleyi (Matthew 1917)

(Figure 25)

Holotype: AMNH 17170, nearly complete upper and lower dentition.

Type locality: Mason Pocket, San Juan Basin, Colorado.

Known age and distribution: Late Tiffanian of Colorado (type locality [Matthew 1917]) and Wyoming ([Gazin 1956a, Gingerich 1976b]).

Referred specimen: UALVP 34882, rm1.

Horizon: Hand Hills West, Upper Level.

Description and discussion:

UALVP 34882 (L=2.6mm, AW=2.6mm, PW=2.2mm) is a right lower first molar, morphologically identical to AMNH 17389 and the published descriptions for Nannodectes gidleyi (Gazin 1956a, Matthew 1917). The m1 of N. gidleyi differs from that of N. simpsoni in being larger and having distinctively squared talonid corners.

This specimen extends the geological time of range of N. gidleyi from the late Tiffanian (Ti4) of Colorado and Wyoming to the middle Tiffanian (Ti3) of Alberta, and indicates the presence of two different species of Nannodectes, and one species of Plesiadapis during the middle Tiffanian (Table 3). This is not consistent with the biostratigraphic zonation of the Paleocene and early Eocene of North America (Gingerich 1976b). Further samples are necessary to review the stratigraphic relationship of these species.

Superfamily Paromomyoidae (Simpson 1940)

Family Picrodontidae Simpson 1935

Genus Zanycteris Matthew 1907

Zanycteris paleocenus Matthew 1907

(Figure 26)

Holotype: AMNH 1780, crushed skull with palate exposed, three molars on both sides and canine on right side preserved.

Type locality: Mason Pocket, Tiffany Formation, Colorado.

Known age and distribution: Middle Tiffanian of Colorado (type locality [Matthew 1907]), and Alberta (UADW-2 locality, Paskapoo Formation, Blindman River [Fox 1990]).

Referred specimen: UALVP 34845, RM1.

Horizon: Hand Hills West, Upper Level.

Description and discussion:

The dimensions of this specimen are L=2.4mm, W=2.0mm. The significant features are: (1) prominent protocone; (2) the paracone is smaller than the metacone; (3) the stylar shelf is narrow, with the metastylar shelf restricted anteriorly; (4) small parastyle; (5) the pre- and postcingulum are distinct, but restricted lingually; (6) the postparacrista extends to the apex of the protocone; and (7) the postmetacrista is shorter than the premetacrista. Although this specimen is worn, it appears not to have had papillated enamel. This tooth position has been adequately described and figured by Matthew (1917), Van Valen (1966), Szalay (1968), Krause (1978), and Gingerich, Houde and Krause (1983).

Zanycteris is known from the middle Tiffanian of Colorado and Alberta. This species is distinct from the only other known Paleocene picrodontid, Picrodus. Picrodus is known from the late Torrejonian to the middle Tiffanian, and is characterized by a more pronounced stylar shelf, reduced paracone and parastylar area, the premetacrista is longer than the postparacrista, and the postparacrista does not extend to the apex of the protocone.

Genus Picrodus Douglas 1908

Picrodus silberlingi Douglas 1908

(Figure 27)

Holotype: CM 1670, right dentary fragment with p4-m1.

Type locality: Silberling Quarry, upper Lebo Formation, Crazy Mountain Field, Sweetgrass County, Montana.

Known age and distribution: Late Torrejonian (middle Paleocene) of Montana (type locality and Gidley Quarry, upper Lebo Formation, Crazy Mountain Field, Sweetgrass County [Douglass 1908, Simpson 1937a]) and Wyoming (Rock Bench Quarry, Fort Union Formation, Polecat Bench [Rose 1981], Swain Quarry, Fort Union Formation, Washakie Basin, Carbon County [Szalay 1968, Rigby 1980], Locality V-82004, Polecat Bench Formation, southern Bighorn Basin [Hartman 1986]); earliest Tiffanian (late Paleocene) of Alberta (Cochrane 2 locality, Porcupine Hills Formation, Cochrane [Krause 1978]); and Wyoming (Keefer Hill locality ["Shotgun local fauna"], Fort Union Formation, Wind River Basin, Fremont County [McGrew and Patterson 1962, Szalay 1968], Bangtail locality, Fort Union Formation, western Crazy Mountain Basin, Park County [Gingerich, et al. 1983]); early Tiffanian of Wyoming (Saddle locality, Fort Union Formation, Bison Basin, Fremont County [McGrew and Patterson 1962, Szalay 1968]); middle Tiffanian of Wyoming (Cedar Point Quarry, Polecat Bench Formation, Bighorn Basin, Bighorn County [Rose 1981]), and Alberta (Hand Hills West locality, lower level, Paskapoo Formation, Hand Hills [Fox 1990]).

Referred specimen: UALVP 34846, LM2.

Horizon: Hand Hills West, Lower Level.

Description and discussion:

The M2 of Picrodus silberlingi is not well known. Unfortunately, much of the crown of this specimen is absent, and it is extensively worn. Overall, this specimen appears to be squared in occlusal view, with papillate enamel.

Picrodus is known from the late Torrejonian to the middle Tiffanian of Montana and Wyoming, and from the earliest Tiffanian to middle Tiffanian of Alberta. The recovery of this specimen supports the age of early Tiffanian for the Lower Level of the Hand Hills Locality, and extends the geographic distribution of Picrodus silberlingi in the early Tiffanian, previously known from Wyoming, to southern Alberta.

Family Paromomyoidae (Simpson 1940)

Genus Ignacius (Matthew and Granger 1921)

Ignacius frugivorus (Matthew and Granger 1921)

(Figure 28a-g; Table 17)

Holotype: AMNH 17368, left maxillary fragment with P2, P4-M2.

Type locality: Mason Pocket, "Tiffany" beds, San Jose Formation, San Juan Basin, Colorado.

Known age and distribution: Earliest Tiffanian (late Paleocene) of Wyoming (Keefer Hill locality ["Shotgun local fauna"], Fort Union Formation, Wind River Basin, Fremont County [Gazin 1971]); early Tiffanian of Montana (Scarritt Quarry, Melville Formation, eastern Crazy Mountain Basin, Sweetgrass County [Simpson 1936]); middle Tiffanian of Alberta (UADW-2 locality, Paskapoo Formation, Blindman River [Fox 1990], Joffre Bridge Roadcut locality, lower level, Paskapoo Formation, Red Deer River [Fox 1990], Hand Hills West locality, upper level, Paskapoo Formation [Fox 1990]), Birchwood locality, Paskapoo Formation, Drayton Valley [Webb in prep.]), North Dakota (Brisbane locality, Tongue River Formation, Williston Basin, Grant County [Holtzman 1978]), and Wyoming (Cedar Point Quarry, Fort Union Formation, northern Bighorn Basin, Bighorn County [Rose 1981]); late Tiffanian of Alberta (Swan Hills site 1, Paskapoo Formation, Swan Hills [Stonley 1988], Police Point locality, Ravenscrag Formation, Cypress Hills [Krishtalka 1973, Krause 1978], Canyon Ski Quarry, Paskapoo Formation, Red Deer [Krause 1978, Fox 1990]), Saskatchewan (Roche Percée Local Fauna, Ravenscrag Formation [Krause 1978], Wyoming (Locality V-77005, Fort Union Formation, eastern Rock Springs Uplift, Sweetwater County [Winterfield 1982, Colorado (type locality [Simpson 1935b]), and Texas (Joe's Bone Bed, Black Peaks Formation, Big Bend National Park [Schiebout 1974]), and North Dakota (Judson locality, Tongue River Formation, Williston Basin, Morton County [Holtzman 1978]).

Referred specimens: UALVP 34897, I1; 34896, P4; 34892, M1; 34895, M2; 34890, M3; 34894, 34899, m2s; 34891, m3.

Horizon: Hand Hills West, Upper Level and Lower Level.

Description and discussion:

The dentition of Ignacius frugivorus has been adequately described and figured by Matthew and Granger (1921), and Krause (1978). The lower molars from the Hand Hills West, Upper Level and Lower Level, differ slightly from previous descriptions. These differences are discussed below. The first description of the I1 of Ignacius frugivorus is provided below.

I1. - UALVP 34897 is a left upper first incisor. The anterocone, laterocone, posterocone, and mediocone are all well developed providing a well-defined seed cup. This specimen is smaller and more narrow than the I1 of Plesiadapis and Nannodectes, and differs from the I1 of Ignacius fremontensis, known from earliest Tiffanian localities, in being narrower, with a better developed laterocone, which extends further labially. This specimen is morphologically identical to undescribed material from the Bison Basin, Wyoming; three upper first incisors included in material labelled Chriacus (CM31036) from the Saddle Locality, and one upper first incisor from the Fort Union Main Saddle locality (pers. obs.). The first upper incisor has not yet been described, as far as I can determine, for Ignacius frugivorus. This specimen, on the basis of morphology, is tentatively identified as the I1 of Ignacius frugivorus.

The m2 is slightly smaller and the m3 is slightly larger than the material referred to Ignacius frugivorus from the late Tiffanian Roche Percée local fauna (Krause 1978). Krause (1978) noted that the paraconid and metaconid are approximately equal in height and separated from each other, differing from Simpson's (1940) observation that the paraconid is absent or fused to the metaconid. The Hand Hills West specimens are similar to the Roche Percée material in these features. The small crenulation seen on the hypoflexid of some of the Roche Percée material is absent on these specimens (Krause 1978).

Superfamily Microsyopoidea Gunnell 1989

Family cf. Palaechthonidae Gunnell 1989

Indeterminate genus and species

(Plate 1E)

Referred specimen: UALVP 34886, LDP4.

Horizon: Hand Hills West, Upper Level.

Description:

The dimensions of this specimen are L=1.7mm, W=1.9mm. The important features of this specimen are as follows: (1) high, sharp cusps; (2) all cusps and conules are well developed; (3) the ectocingulum is reduced; (4) squared in occlusal view; (5) the trigon is small but deeply basined; (6) the paracone and metacone are offset slightly posteriorly from the paraconule and metaconule; (7) the precingulum and postcingulum are well developed, almost shelf-like; (8) the parastylar area is expanded anterolabially, with a distinct parastyle; (9) the preparaconule crista and preparacrista form strong crests; (10) the paracone and metacone are connected through approximately half of their height by a crest; (11) the paracone is slightly compressed anteroposteriorly; (12) the metacone is slightly compressed linguolabially; and (13) the postmetaconule appears to have extended posteriorly, likely to an expanded metastylar area, absent on this specimen.

Discussion:

The suborder Plesiadapiformes has two superfamilies, the Microsyopoidea and the Plesiadapoidea (Gunnell 1989). The P4s of Plesiadapiformes are characterized as being premolariform to semi-molariform, with a reduced protocone (Bown and Rose 1976, Gunnell 1989). The P4s of the Microsyopoidea and the Plesiadapoidea differ in the development of the metacone, parastyle, and paraconule, and their relationship to the paracone.

Within the Superfamily Plesiadapoidea, the condition of the P4 ranges from the metacone being weak to absent in the Subfamily Paromomyinae, to the metacone being well developed in the Subfamily Phenacolemurinae.

Within the Superfamily Microsyopoidea, there are two families, the Palaechthonidae and the Microsyopidae. The Palaechthonidae demonstrate variation in the features of the P4. In Palaechthon (Subfamily Palaechthoninae) the metacone is small and connected to the paracone, and the parastyle is distinct and separated. In Palaenochtha, the metacone is distinct and separated from the paracone, as is the parastyle, and there is a distinct paraconule. In Plesiolestes (Subfamily Plesiolestinae), the metacone is distinct and separated from the paracone, the parastyle is distinct but not separated from the paracone, and there is a distinct paraconule. In the Microsyopidae, the metacone is small to absent and not separated from the paracone, and the parastyle is weak.

This specimen is tentatively referred to the Family Palaechthonidae, indeterminate genus and species, based on the prominent paracone and metacone, distinct parastyle and paraconule offset from the paracone.

Family cf. Palaechthonidae Gunnell 1989

Indeterminate genus and species

(Plate 1F)

Referred specimen: UALVP 34885, ldp4.

Horizon: Hand Hills West, Upper Level.

Description:

The dimensions of this specimen are L=1.8mm, AW=1.0mm, PW=1.2mm. The significant features of this specimen are as follows: (1) semi-molariform; (2) the paraconid small, distinct, and set off anteriorly from the metaconid; (3) the talonid is deeply basined, with the entoconid as the highest cusp; (4) the hypoconid is distinct; (5) the postcingulid is reduced; (6) the metaconid is the highest cusp and oriented slightly labially; (7) the protoconid is well-developed, with a relatively distinct protocristid; and (8) the cristid obliqua is distinct.

Discussion:

The p4 of the Superfamily Plesiadapoidea is characterized as premolariform, and the paraconid and metaconid are weak to absent, with two talonid cusps (Gunnell 1989). The p4 of the Superfamily Microsyopoidea is characterized as premolariform (Palaenochtha) or semi-molariform (Palaechthon, Plesiolestes), the paraconid is weak, the metaconid low and cuspate to absent, with two talonid cusps (Bown and Rose 1976, Gunnell 1989).

The Family Palaechthoninae (Microsyopoidea) is characterized by a molariform p4, more acute cusps, and the presence of a paraconid. The genus Plesiolestes is characterized by a well-developed metaconid (present in this specimen), a strongly developed basin, and often a distinct entoconid. These features are typically absent in Palaechthon.

The p4 of the Family Microsyopidae (Microsyopoidea) is characterized as semi-molariform, with a distinct paraconid, and well-developed talonid cusps (Bown and Rose 1976). Microsyops is characterized by a distinct paraconid, and the metaconid is variably developed.

The dimensions of this specimen (L=2.0mm, W=1.1mm) indicate that it is smaller than the p4 of Microsyops, larger than the p4 of Micromomys (Fox 1984c), larger than the p4 of Palaechthon woodi (Bown and Rose 1976), smaller than the p4 of P. nacimienti (Bown and Rose 1976), and within the size range for the p4 of P. alticuspis (Bown and Rose 1976, Gunnell 1989).

The primitive features of this specimen are the high cusps, and the distinct paraconid. This specimen is tentatively referred to the Family Palaechthonidae, indeterminate genus and species, based on the distinct paraconid, metaconid, entoconid, and the deeply basined talonid.

Family cf. Microsyopidae Osborn and Wortman 1892

Indeterminate genus and species

(Plate 1G)

Referred specimen: UALVP 35186, LDP4.

Horizon: Hand Hills West, Upper Level.

Description:

The dimensions of this specimen are L=1.8mm, W=1.6mm. The important features of this specimen are as follows: (1) high, sharp cusps; (2) all cusps and conules are well developed; (3) the paracone is connate and leans anteriorly; (4) the metacone is compressed labiolingually; (5) the paraconule is distinct; (6) the parastylar area is not expanded; (7) the parastyle is absent; and (8) the precingulum and postcingulum appear to have been well developed.

This specimen differs from UALVP 34886, referred to the Family Palaechthonidae, in (1) being more elongated and narrow; (2) having a straight stylar shelf; (3) the absence of a parastyle; (4) the restriction of the precingulum posteriorly; (5) the postmetaconule crista not extending to the postcingulum; and (6) the preparaconule crista not extending to precingulum.

Discussion:

The P4 of the Superfamily Microsyopoidea is characterized as being premolariform to semi-molariform, with a reduced protocone (Bown and Rose 1976, Gunnell 1989).

The Family Palaechthonidae demonstrates variation in the features of the P4 as follows: (1) the metacone is small and connected to the paracone, with a distinct parastyle that is separated from the paracone; (2) the metacone is distinct and separated from the paracone with a distinct paraconule; or (3) the metacone distinct and separated from the paracone, with a distinct parastyle and paraconule (Gunnell 1989).

In the Family Microsyopidae, the metacone is small to absent, connected to the paracone, with a weak parastyle (Gunnell 1989). The primitive stages of the Microsyopidae are characterized by the lack of a stylar shelf (Szalay 1969).

This specimen is tentatively referred to the Family Microsyopidae, indeterminate genus and species, based on the absence of the parastyle, and the reduced stylar shelf.

Order "Condylarthra"

Family Phenacodontidae Cope 1881

Genus Ectocion Cope 1882

Ectocion cedrus Thewissen 1990

(Figure 29a-c; Table 18)

Holotype: UM 82085, left dentary with p2 to m3 and alveoli for c1 and p1.

Type locality: Cedar Point Quarry, Polecat Bench Formation, Fort Union Formation, Bighorn Basin, Bighorn County, Wyoming.

Known age and distribution: Middle Tiffanian of Wyoming (type locality, Wind River Basin [Gingerich 1976c]), North Dakota (Brisbane locality, Tongue River Formation, Williston Basin, Grant County [Holtzman 1978]), and Alberta (UADW-2 locality, Paskapoo Formation, Blindman River [Fox 1990], Hand Hills West Upper Level, Paskapoo Formation [Fox 1990]; Birchwood locality, Paskapoo Formation, Drayton Valley [M.W. Webb in prep.]).

Referred specimens: UALVP 34916, 34917, 34909, P3s; 34908, DP3; 34913, 34914, M1s; 34911, 34941, 34912, 34915, M2s; 34942, M3; 34919 rm1-m2; 34920, p3; 34944, 34921, p4s; 34945, dp4; 34918, m2; 34943, m3.

Horizon: Hand Hills West, Upper Level.

Description:

The upper dentition and lower dentition of *Ectocion cedrus* have been adequately described and figured by Cope (1882), Gazin (1956a), West (1976, 1977), Krause and Gingerich (1983), and Thewissen (1990). The upper molars are characterized by prominent styles, and the preprotocrista and postprotocrista are well developed. The lower molars are characterized by a low and weak paraconid, and the trigonid is shallow. The molars of *Ectocion cedrus* are intermediate in size, smaller than those of *E. collinus*, and larger than those of *E. osbornianum* (the dimensions for M3 are not available as the enamel is very worn on this specimen).

The DP3, p4 and dp4 of *E. cedrus* are not well known, and more detailed descriptions are provided below.

DP3. - The deciduous dentition of the Phenacodontidae has been extensively described by West (1971). However, a detailed description of DP3 of *E. cedrus* (referred to *E. wyomingensis* by West, 1971) was not provided. The following features were recognized for the DP3 of *E. osbornianum* and found in UALVP 34908: (1) the paracone and metacone are distinctly separated; (2) an incipient paraconule and preprotocrista; and (3) an enclosed trigon basin, due to the absence of postprotocrista and metaconule (West 1971). These features are absent in the early Tiffanian *E. collinus*. Although this specimen bears a striking resemblance to the DP3 of the late Tiffanian *E. osbornianum*, it is considerably larger.

p4. - The following features of p4 were recognized in both E. osbornianum and the Hand Hills West, Upper Level specimens: (1) the entoconid and the mesoconid are well developed; (2) the paracristid forms a strong crest with small cuspules; (3) the paraconid is high, higher than in E. mediotuber (Thewissen 1990); and (4) the talonid is narrow. This specimen is similar morphologically to, but larger than the p4 of E. osbornianum recovered from the late Tiffanian Roche Percée (see Krause 1986) and Swan Hills (see Stonely 1988) localities. It is significantly smaller than E. collinus from the earliest Tiffanian Douglass Quarry (see Krause 1986) and Cochrane 2 localities (see Youzwyshyn 1988).

dp4. - UALVP 34945 is an isolated right deciduous lower fourth premolar, and possesses these features as cited by West (1971) for E. cedrus: (1) triangular paraconid, (2) prominent metastylid; (3) the absence of the entostylid (present but small on this specimen); (4) cuspate cristid obliqua; and (5) the hypoconulid is equidistant from entoconid and hypoconid. The parastylid is well developed, equal in height to the paraconid. This feature is not mentioned by West (1971). E. cedrus differs from E. osbornianum in the hypoconulid being closer to the entoconid, with a better developed paraconid and entostylid.

Discussion:

Thewissen (1990) revised the genus Ectocion, and recognized two middle Tiffanian species, E. cedrus (includes E. wyomingensis (West 1976) in part, and ?Phenacodus (Simpson 1937a)) and E. mediotuber. Remains of E. cedrus are found within sediments of the middle Tiffanian *Plesiadapis rex* zone (Ti3) and characteristic of poorly drained deposits, while *E. mediotuber* is within the late Tiffanian *Plesiadapis churchilli* zone (Ti4), and are characteristic of well-drained deposits (Thewissen 1990). The *Ectocion* material from the Upper Level is referrable to *E. cedrus*, and the Hand Hills West is a poorly drained deposit.

Ectocion sp.

Horizon: Hand Hills West, Lower Level.

Description and discussion:

This material represents lower molar fragments of Ectocion, based on the size and crenulated enamel. These specimens are not worn but are highly fragmented. Identification below the genus level is not possible.

Family Arctocyonidae Murray 1866

Subfamily Oxyclaeninae Matthew 1917

Genus Claenodon Scott 1892

Claenodon sp.

(Figure 30)

Referred specimen: UALVP 34922, M3.

Horizon: Hand Hills West, Upper Level.

Description and Discussion:

The significant features of this specimen are: (1) paracone and metacone are well developed; (2) conules are well developed; (3) the paraconule is reduced in comparison to the metaconule; and (4) the ectocingulum, preparacrista, and centrocrista are well developed and crenulated. The reduced hypocone, the slightly expanded parastylar area, the absence of styles, and the wrinkled enamel are characteristic of this genus (Krause and Gingerich 1983).

The dimensions of this specimen are L=7.8mm, W=10.7mm. The upper molars of this genus are typically separated on the basis of size, as very few reliable specific characteristics are known (Krause and Gingerich 1983). This specimen is larger than the m3 of Claenodon montanensis (Gidley 1919), C. acrogenius (Gazin 1956a), and C. ferox (Simpson 1937a), and comparable in size to the m3 of Claenodon sp. from the late Tiffanian Swan Hills locality (see Stonely 1988).

Family Hyopsodontidae Lydekker 1889

Genus Dorraletes Gingerich 1983

Dorraletes diminutivus (Dorr 1952)

(Figure 31)

Holotype: UM 27231, left maxillary fragment with P4-M2.

Type locality: Dell Creek Quarry, Hoback Formation, Hoback Basin, Sublette County, Wyoming.

Known age and distribution: Middle Tiffanian of Wyoming, (Type Chappo locality, Wasatch Formation, Lincoln County [Gingerich 1983, Gunnell 1994]), North Dakota (Brisbane locality, Tongue River Formation, Grant County [Holtzman 1978]), and Alberta (Birchwood locality, Paskapoo Formation, Drayton Valley [M.W. Webb in prep.]); late Tiffanian of Wyoming (type locality [Dorr 1952], and North Dakota (Judson locality, Tongue River Formation, Williston Basin, Morton County [Holtzman 1978]).

Referred specimens: UALVP 35107, 35212, M1s.

Horizon: Hand Hills West, Upper Level and Lower Level.

Description:

The dimensions of these specimens are (UALVP 35107 L=2.0mm, W=2.6mm, UALVP 35212 L=2.0, W=2.5mm). The important features of UALVP 35212, from the Lower Level, are: (1) the paracone, metacone and protocone are well-developed; (2) strong pre- and postparacrista; (3) the metacone is compressed anteroposteriorly; strong pre- and postmetacrista; (4) the conules are prominent; (5) the parconule is further labial than the metaconule; (6) small, distinct hypocone; (7) small pericone, directly anterior to the protocone; and (8) preparaconule crista and postmetaconule crista form well-developed crests. UALVP 35107, from the Upper Level, is worn and differs in being slightly larger, with higher cusps, and a slightly deeper ectoflexus.

These specimens are morphologically similar to the M1 of Dorraletes diminutivus (UM 27231, UM 72069, figure 7 and 8, Gingerich 1983, pp:245-246). They differ in the postmetacrista being directed labially, rather than directly posteriorly as in UM 27231 and UM 72069.

Discussion:

Gingerich (1983) described the genus Dorraletes as a small hyopsodontid condylarth characterized by distinct conules, a small and distinct hypocone, and a small pericone, and referred the holotype of Haplaletes diminutivus (Dorr 1952) to this genus. Gingerich (1983) noted that Dorraletes differs from Haplaletes in being much smaller, having more nearly symmetrical M1 and M2, a small hypocone, smaller pericone, and occluding cusps more rounded and less angular.

The recovery of Dorraletes diminutivus from the Hand Hills West, Upper Level, and the Birchwood locality (M.W. Webb in prep.), extends its geographic distribution to Alberta in the middle Tiffanian, and its recovery from the Hand Hills West Lower Level extends its geological time range to the early Tiffanian.

Order Dermoptera Illiger 1811

Family Plagiomenidae Matthew 1918

Genus Elpidophorus Simpson 1927

Elpidophorus elegans Simpson 1927

(Figure 32a-e; Table 19)

Holotype: AMNH 15541, right dentary fragment with m1-m2.

Type locality: Erickson's Landing, Paskapoo Formation, Red Deer River, Alberta.

Known age and distribution: Early Tiffanian (late Paleocene) of Montana (Scarritt Quarry, Melville Formation, eastern Crazy Mountain Basin, Sweetgrass County [Szalay 1969]); middle Tiffanian of Alberta (type locality [Simpson 1927a], UADW-1, UADW-2 localities, Paskapoo Formation, Blindman River [Fox 1990], Birchwood locality, Paskapoo Formation, Drayton Valley [M.W. Webb in prep.], Joffre Bridge Roadcut, lower level, and Joffre Bridge Mammal Site No. 1 localities, Paskapoo Formation, Red Deer River [Fox 1990]) and Wyoming (Cedar Point Quarry, Fort Union Formation, northern Bighorn Basin, Bighorn County [Rose and Simons 1977]); late Tiffanian of Alberta (Police Point locality, Ravenscrag Formation, Cypress Hills [Krishtalka 1973]).

Referred specimens: UALVP 35187, LDP2; 34999, 35045, M1s; 35000, M2; 35268, i1; 35264, 35271, p1s; 35050, rp3; 35002, 35003, dp3s; 35049, rp4; 35001, m2.

Horizon: Hand Hills West, Upper Level and Lower Level.

Description and discussion:

The upper molars and lower molars of Elpidophorus elegans have been adequately described and figured by Simpson (1927a, 1935, 1927), Szalay (1969), Krishtalka (1973), and Rose and Simons (1977). The following tooth positions are further described p1, p3, dp3, and p4.

p1. - The important features of these specimens are: (1) premolariform; (2) wedge-shaped protoconid that extends anteriorly over the root; (3) small talonid with a centrally located cusp; and (4) a well developed crest that extends from the talonid to the apex of the protoconid.

p3. - The significant features of this specimen are: (1) molariform; (2) paraconid is small but distinct, and located on the anterior most edge of the cingulid; (3) the paracristid and cristid obliqua are well developed, as in p4; and (4) the subconical hypoconid has a wider base than the small and conical entoconid.

dp3. - The distinctive features of these specimens are: (1) the talonid has four cusps that are inclined anterolingually; (2) the protoconid is high, narrow and centrally located; (3) the paraconid is small and conical; (4) the metaconid is a small cusp posterolingually on the protocristid extends posterior and lingual; (5) there is a small cuspule posterior and labial to the protoconid, further posterior and labial to the metaconid; (6) the paracristid is well developed and extends anterior to the paraconid; (7) the precingulid extends along the anteriolabial edge of the crown between the paraconid and protoconid; (8) the postcinulid is expanded posterolabially to form a distinct shelf; (9) the talonid is small with a small crescentric hypoconulid (the talonid is worn and there may be a small entoconid); and (10) the entocristid and cristid obliqua are well developed and enclose the talonid basin.

The p3 differs from the dp3 in the absence of the metaconid and the accessory cuspule posteriolabial to the protoconid and metaconid, having a reduced postcingulid, and being more elongated anteroposteriorly.

p4. - UALVP 35049 is characterized by the following features: (1) molariform with the trigonid elongated anteroposteriorly; (2) the talonid is short (approximately half the length of the trigonid), squared, sloped labially and slightly basined; (3) the paraconid is prominent and sloped anteriorly; (4) the hypoconid is subconical and widely based; (4) the paracristid is strong; (5) the precingulid is well developed and extends from the base of the paraconid to the protoconid; (7) the entoconid is conical; (8) the hypoconulid is absent; and (9) the cristid obliqua is distinct.

There are no significant differences between the samples from the Upper Level and the Lower Level.

Order Uncertain

Indeterminate genus and species

(Figure 33a,b;Table 20)

Referred specimens: UALVP 35046, 35047, 35048, 35188, I1's.

Horizon: Hand Hills West, Lower Level.

Description:

The distinctive features of these specimens are: (1) small with high, sharp cusps; (2) the laterocone is well-developed and oriented posterior and distally; (3) the posterocone is well developed and in line with the well developed anterocone; (4) the posterocrista and anterocrista are well developed; and (5) the crista along the posterocone, extending to the base of the crown, possesses a small cuspule. This cuspule is variably developed on the specimens and is located at the base of the posterocone or slightly medial.

Discussion:

These specimens are similar to the incisors of dermopterans and primates in terms of cusp morphology, but differ significantly from these groups in their small size and the primitive condition of the cusps. Elphidophorus minor (Simpson. 1937a,b) is smaller and more primitive than E. elegans, but is only known from the lower dentition. Rose and Simons (1977) noted that the deciduous incisors of Plagiomene are more cuspate than the permanent incisors, but the cusps are aligned along the labial edge. These specimens do not differ in colouration or wear patterns as is characteristic of deciduous teeth (West 1971). The relationship between dermopterans and primates has been the subject of much discussion. Lipotyphylans are small "insectivores" and have been suggested to be closely related to the ancestry of these groups, and are well represented in the faunal assemblage of Tiffanian localities. These specimens likely belong to one of these groups, but further comparative material in association with other identifiable dental elements is necessary for identification.

Family Pantolestidae Cope 1884

Genus Propalaeosinopa Simpson 1935

Propalaeosinopa septentrionalis Russell 1929

(Table 21)

Holotype: UALVP 126, left dentary fragment with m3.

Type locality: Cochrane site 1, Porcupine Hills Formation, southwestern Alberta.

Known age and distribution: Late Torrejonian (middle Paleocene) of Montana (Gidley Quarry, Upper Lebo Formation, Crazy Mountain Field, Sweetgrass County [Simpson 1935a]) and Wyoming (Swain Quarry, Fort Union Formation, Washakie Basin, Carbon County [Rigby 1980], localities V-82004, V-82006, V82040, Polecat Bench Formation, southern Bighorn Basin [Hartman 1986]); earliest Tiffanian (late Paleocene) of Alberta (type locality [Russell 1929]), Montana (Douglass Quarry, Melville Formation, eastern Crazy Mountain Basin, Sweetgrass County [Krause and Gingerich 1983]), and Wyoming (Locality V-82015, Polecat Bench Formation, southern Bighorn Basin [Hartman 1986]); early Tiffanian of Montana (Scarritt Quarry, Melville Formation, eastern Crazy Mountain Basin [Simpson 1936a,b]); middle Tiffanian of Alberta (UADW-2 locality, Paskapoo Formation, Blindman River [Fox 1984a], Joffre Bridge Roadcut locality, lower level, Paskapoo Formation, Red Deer River [Fox 1990], Burbank localities, Paskapoo Formation, Blindman River [Fox 1990], Birchwood locality, Paskapoo

Formation, Drayton Valley [M. W. Webb in prep.]), and North Dakota (Brisbane locality, Tongue River Formation, Grant County [Holtzman 1978]); late Tiffanian of North Dakota (Judson locality, Tongue River Formation, Morton County [Holtzman 1978]) and Alberta (Police Point Locality, Ravenscrag Formation, Cypress Hills [Krishtalka 1973]).

Referred specimens: UALVP 35051, 35053, 35057, 35061, 35055, 35058, 35214, M1s; 35054, 35056, 35062, 35197, M2s; 35203, MX, 35215, MX, 35216, MX, 35052, M3; 35059, 35060 m3s.

Horizon: Hand Hills West, Upper Level and Lower Level.

Description:

M1. - These specimens are moderately wide, with a well-developed paracone and metacone. The metacone is compressed anteroposteriorly, the paracone is slanted slightly anteriorly, and the protocone is prominent with a wide base. The paraconule is small and conical, the metaconule is larger and pyramidal. The paraconule is situated further lingually than the metaconule. The hypocone is distinct and situated posterolingually to the protocone. The parastyle is small and cuspate, and the postmetacrista is strong. The precingulum is well developed and is restricted anterior to the protocone. The postcingulum is well developed and extends to the base of the metaconule. The stylar shelf is reduced with a shallow ectoflexus.

M2. - These specimens are fragmentary, and the enamel is worn. The crown lingual to the paraconule is represented. The protocone is more narrow, the hypocone is small and conical, and the precingulum extends further lingually to the base of the protocone than on M1. UALVP 35197 (L=2.6mm, W=2.8mm) from the Lower Level is the most nearly complete specimen and appears to be slightly smaller than the material from the Upper Level.

M3. - UALVP 35052 is a very worn isolated right upper third molar, with much of the enamel missing. The paracone and protocone are well developed, the metacone is small, cuspate, and slanted anteriorly. The conules appear to have been moderately developed. The parastylar shelf is prominent and expanded anterolabially. The precingulum and postcingulum are present but worn.

m3. - The trigonid is higher than the talonid, with high sharp cusps. The protoconid and metaconid are well developed, with the metaconid being the highest cusps, and the paraconid is low and laterally compressed. The entoconid is cuspate and is slightly higher than the hypoconid. The hypoconulid is laterally compressed and centrally located on the talonid. The precingulid is distinct, distinguishing it from m1. The entocristid is straight, and the cristid obliqua is slanted lingually as in m2.

Discussion:

Youzwyshyn (1988) compared UALVP126, the holotype of "Diacodon septentrionalis" (Russell 1929) from the earliest Tiffanian Cochrane 1 locality and the paratypes UALVP333 from the earliest Tiffanian Cochrane 2 locality, to the m3 of Propalaeosinopa diluculi from the late Tiffanian Gidley Quarry (Simpson 1937a). Youzwyshyn (1988) removed the paratypes from "Diacodon septentrionalis" and described them as unidentified genera and species of palaeoryctid (sp.1 and sp.2), and referred the holotype to the genus Propalaeosinopa (Simpson 1935a). Russell's (1929) P. septentrionalis has priority over P. diluculi (Bessoecetor diluculi Simpson 1937a). Van Valen (1967) suggested the synonomy of Propalaeosinopa diluculi and "Bessoecetor" thompsoni (Simpson 1936) with P. albertensis (Simpson 1936). Youzwyshyn (1988) suggested that P. albertensis is distinct from P. septentrionalis (previously P. diluculi).

The material from the Hand Hills West, Upper Level and Lower Level is morphologically identical to homologous teeth from the earliest Tiffanian Cochrane 2 referred to Propalaeosinopa septentrionalis (Youzwyshyn 1988).

Family Palaeoryctidae Winge 1917

Genus *Pararyctes* Van Valen 1966

Pararyctes pattersoni Van Valen 1966

(Plate 1H; Table 22)

Holotype: UW 2002, left M1.

Type Locality: Saddle locality, Fort Union Formation, Bison Basin, Fremont County, Wyoming.

Known age and distribution: Earliest Tiffanian (late Paleocene) of Alberta (Cochrane 2 locality, Porcupine Hills Formation, Cochrane [Van Valen 1966, Youzwyshyn 1988]); early Tiffanian of Wyoming (type locality [Van Valen 1966]); middle Tiffanian of Alberta (UADW-2 locality, Paskapoo Formation, Blindman River [Fox 1990]; Joffre Bridge Roadcut locality, lower level, Paskapoo Formation, Red Deer River [Fox 1990]; Birchwood locality, Paskapoo Formation, Drayton Valley [M.W. Webb in prep.]) and North Dakota (Brisbane locality, Tongue River Formation, Williston Basin, Grant County [Holtzman 1978]); late Tiffanian of Alberta (Police Point locality, Ravenscrag Formation, Cypress Hills [Krishtalka 1973, Fox 1990]) and Saskatchewan (Roche Percée Local Fauna, Ravenscrag Formation [Fox 1990]).

Referred specimens: UALVP 35155, M1; 35202, 35088 M2s; 35076, right dentary fragment with p5-m3; 35079, left dentary fragment with m1-m2; 35077, dp4; 35084 m1; 35082, 35078, 35081, 35083, 35086 m2s; 35087, m3.

Horizons: Hand Hills West, Upper Level and Lower Level.

Description and discussion:

Pararyctes pattersoni is known from the early Tiffanian of Wyoming, the middle Tiffanian of North Dakota, and the earliest to late Tiffanian of western Canada. The dentition of Pararcytes pattersoni has been adequately described and figured by Van Valen (1966) and Holtzman (1978).

There is no significant difference between the samples from the Upper Level and the Lower Level.

Pararyctes sp.1

(Table 23)

Referred specimens: UALVP 35085, left dentary fragment with m1- trigonid of m2.

Horizons: Hand Hills West, Upper Level and Lower Level.

Description and discussion:

UALVP 35085 is a left dentary fragment with m1 and the trigonid of m2. The lower molars are morphologically identical to *Pararyctes pattersoni* from earliest Tiffanian Cochrane 2 locality, and the Hand Hills West, Upper Level and Lower Level, but are approximately 12% smaller (Youzwyshyn 1988). These specimens may be referrable to *Pararyctes pattersoni*, but further comparative samples are necessary to refer these specimens to *Pararyctes pattersoni*.

Pararyctes sp.2

(Table 23)

Referred specimens: UALVP 35157, lm2; 35158, rm3.

Horizon: Hand Hills West, Upper Level.

Description and discussion:

These specimens are morphologically identical to Pararyctes pattersoni from the Hand Hills West, Upper Level and Lower Level, but are approximately 15% larger. Youzwyshyn (1988) referred a lower molar to m1 or m2 of Pararyctes rutherfordi from the earliest Tiffanian Cochrane 2 locality. Pararyctes rutherfordi is characterized as being similar to Pararcytes pattersoni, but 40% larger (Youzwyshyn 1988). The lower molar from Cochrane 2 is fragmentary and worn; better comparative samples are necessary to refer the Hand Hills West, Upper Level material below the genus level.

Pararyctes sp.

(Plate 2A; Table 23)

Referred specimen: UALVP 35156, LM2.

Horizon: Hand Hills West, Upper Level.

Description and discussion:

UALVP 35156 is morphologically identical to the type specimen of Pararyctes rutherfordi from the earliest Tiffanian Cochrane 2 locality (Youzwyshyn 1988). The M2 of Pararyctes rutherfordi is described as being similar to Pararcytes pattersoni, with a relatively broader postcingulum on M2, and approximately 40% larger (Youzwyshyn 1988). This specimen is referred to Pararyctes sp., and is 150% larger than Pararyctes rutherfordi.

Genus Palaeoryctes Matthew 1913

Palaeoryctes sp., cf. P. punctatus Van Valen 1966

(Plate 2B, 2C)

Type of Palaeoryctes punctatus: AMNH 15850, right dentary fragment with damaged p4-m3 and associated right maxillary fragment with damaged M1-M3, distal end of left humerus, proximal end of ulna.

Type locality: Site in the head of Big Sand Coulee, Willwood Formation, Clark's Fork Basin, Wyoming.

Known age and distribution of Palaeoryctes punctatus: Middle Tiffanian (late Paleocene) of North Dakota (Brisbane locality, Tongue River Formation, Williston Basin, Grant County [Holtzman 1978]); ?latest Tiffanian of Wyoming (?Princeton Quarry, Polecat Bench Formation, Bighorn Basin, Park County [Rose 1981]); middle Clarkforkian (earliest Eocene) of Wyoming (Locality SC-136, Willwood Formation, Clark's Fork Basin [Rose 1981]); late Clarkforkian of Wyoming (type locality [Van Valen 1966, Rose 1981]).

Referred specimens: UALVP 35153, LM3; 35154, rm1.

Horizon: Hand Hills West, Upper Level.

Description and discussion: The dimensions of the M3 are L=1.8mm, W= 3.5mm, and the m1 are L=2.1mm, AW=1.5mm, PW=1.2mm. These specimens are identical to homologous tooth positions referred to Palaeoryctes sp., cf. P. punctatus by Youzwyshyn (1988).

Youzwyshyn (1988) described material from the earliest Tiffanian Cochrane 2 locality that is larger than Palaeoryctes puercensis, with a less antero-posteriorly compressed trigonid, relatively lower talonid, and distinct paraconid. The lower molars were compared to Palaeoryctes punctatus from the middle Tiffanian Brisbane locality (Holtzman 1978), and were morphologically similar, but smaller. This material was referred to Palaeoryctes sp., cf. P. punctatus (Youzwyshyn 1988).

Family Pentacodontidae Simpson 1937

Genus Bisonalveus Gazin 1956

Bisonalveus sp., cf. B. browni Gazin 1956

(Figures 34a, b; Table 24)

Type of Bisonalveus browni: USNM 20928, left dentary with p4-m3 and posterior alveolus for p3.

Type locality: Saddle locality, Fort Union Formation, Bison Basin, Fremont County, Wyoming.

Known age and distribution of Bisonalveus browni: Earliest Tiffanian (Late Paleocene) of Montana (Douglass Quarry, Melville Formation, eastern Crazy Mountain Basin, Sweetgrass County [Krause and Gingerich 1983]), and Alberta (Cochrane 2, Paskapoo Formation, Cochrane [Youzwyshyn 1988]); early Tiffanian of Wyoming (Saddle Locality, Fort Union Formation, Bison Basin, Fremont County [Gazin 1956]); middle Tiffanian of Alberta (Hand Hills West Upper Level, Paskapoo Formation [Fox 1990].

Referred specimens: UALVP 35004, 35005, P4s; 35011, 35012, 35016, 35044, 35193, 35063, 35070, 35210, 35159, 35193, M1s; 35013, 35014, 35015, 35066, 35067, 35068, 35071, 35072, 35043, 35065, M2s; 35017, 35064, M3s; 35007, 35008, 35009, p4s; 35006, 35010, dp4s; 35018, 35019, 35020, 35021, 35023, 35024, 35031, 35025, m1s; 35022, 35027, 35028, 35029, 35030, 35033, 35026, 35041, m2s; 35032, 35034, 35035, 35036, 35037, 35038, 35039, 35040, 35042, m3s.

Horizons: Hand Hills West, Upper Level and Lower Level.

Description:

The dentition of Bisonalveus browni has been adequately described by Krause and Gingerich (1983), and Gazin (1956). More detailed descriptions of P4 and DP4 are provided, as these tooth positions are not well known.

P4. - The distinctive features of the P4 are: (1) molariform; (2) "hourglass" shaped in occlusal view; (3) slightly smaller than M1; (4) the paracone is larger than the metacone and protocone; (5) the paracone and metacone are appressed; (6) the parastyle is small and distinct; (7) prominent paraconule; and (8) the precingulum and postcingulum are well developed.

DP4. -The distinctive features of the DP4 are: (1) the protoconid is the highest cusp, slanted labially; (2) the paraconid is approximately 3/4 of the height of the protoconid and slanted anteriorly; (3) the metaconid is compressed labiolingually and is located slightly posterior to and equal in height to the protoconid; and (4) the entoconid is cuspate and approximately equal in height to the hypoconid.

Discussion:

There are no significant differences between the samples from the Upper Level and the Lower Level. The lower molars of the Hand Hills West differ from Bisonalveus gracilis n. sp. from the middle Tiffanian Birchwood locality (M.W. Webb in prep.) in being more elongate, with the paraconid situated further labially on m1 and m3. The p4 is more elongate, smaller, with a well developed precingulid. Webb (in prep.) referred undescribed material, previously referred to Bisonalveus sp., cf. B. browni, from the middle Tiffanian UADW-2 locality to B. gracilis.

The recovery of Bisonalveus sp., cf. B. browni from the earliest Tiffanian Cochrane 2 locality of Alberta (Youzwyshyn 1988), extended the northern distribution of this species. The recovery of Bisonalveus sp., cf. B. browni from the Lower Level extends the geographic distribution of this species in the early Tiffanian to Alberta. The recovery of Bisonalveus sp., cf. B. browni from the Upper Level extends its geological time range to the middle Tiffanian (Ti3) (Table 31).

Family Apatemyidae Matthew 1909

indeterminate genus and species

(Figure 35a-f)

Referred specimens: UALVP 35260, LI1; 35267, lp2; 35265, 35266, p4's.

Horizon: Hand Hills West, Upper Level and Lower Level.

Description and discussion:

I1. - UALVP 35260 is a left upper first incisor (L=2.4mm, W=1.8mm, H=0.9mm) from the Hand Hills West, Upper Level. This specimen is characterized by a large anterocone, curved anteriorly, and a small posterocone. Gingerich and Rose (1982) noted that the incisors of the Apatemyidae are similar to primitive Microsyopidae. This specimen is likely referrable to the genus Labidolemur based on size and the age of middle Tiffanian for the Upper Level. Labidolemur soricoides (Matthew and Granger 1921) from the middle Tiffanian is known only from the lower dentition. L. kayi and L. serus from the late Tiffanian, are larger than L. soricoides and are represented by the lower and upper dentitions (Gingerich and Rose 1982, Gingerich 1982). This specimen is within the size range expected for L. soricoides, smaller than L. kayi (I1 L=3.1mm, W=1.4mm, H=4.1mm, Gingerich and Rose 1982), and L. serus (I1 L=2.7-3.1mm, W=1.2-1.5mm, Gingerich 1982).

p2. - UALVP 35267 (L=3.5mm, W=1.8mm) is an isolated left lower second premolar from the Hand Hills West, Lower Level. The distinctive features of this specimen are: (1) single rooted; (2) prominent posterior cuspule; (3) small cuspule, lingual to the posterior cuspule along the base of the enamel; (4) the protoconid is slanted labially; (5) the crown extends anteriorly over the root; and (6) there is a well-developed crista that extends from the posterior cuspule along the protoconid, and descends anterior then labially from the protoconid.

This specimen differs from the p2 from the earliest Tiffanian Cochrane 2 locality, referred to *Jepsenella* sp,. cf. *J*. *praepropera* (UALVP 28575, L=2.9mm, W=1.4mm, Youzwyshyn 1988), in the following features: (1) larger; (2) relatively lower and wider; (3) the posterior cuspule and cristae are stronger; (4) the presence of a small cuspule lingual to the posterior cuspule; (5) protoconid slanted further labially; and (6) resembles an equilateral triangle in lateral view, unlike the p2 of *J*. sp., cf. *J*. *praepropera*, which resembles an isosceles triangle in lateral view.

UALVP 35267 is similar to the p2 of late Tiffanian *Labidolemur* *kayi* (L=2.3mm, W=1.0mm, Gingerich and Rose 1982) and *L*. *serus* (L=1.8-2.3mm, W=0.9-1.1mm, Gingerich 1982) in terms of the wedge-shaped morphology, but is larger. The p2 of the middle Tiffanian *Labidolemur* *soricoides* is not known.

p4. - UALVP 35265 is the labial part of an isolated left lower fourth premolar. UALVP 35266 is an isolated right lower fourth premolar. The p4's of *Labidolemur* *kayi* are characterized by a simple blunt crown, rounded protoconid and keeled talonid

(Gingerich and Rose 1982). The holotype of L. kayi (Simpson 1929) has a single-rooted p4; specimens from the Clarks Fork Basin have double-rooted p4's, with the roots fused along their length (Gingerich and Rose 1982). These specimens are double-rooted and similar in terms of morphology to L. kayi (L=1.2mm, W=0.8mm), but slightly longer. The p4 of L. soricoides and L. serus are not known.

The Apatemyidae are represented by the genus Jepsenella in the earliest Tiffanian (Simpson 1940, McKenna 1963, Szalay 1968), the genera Labidolemur (Simpson 1929, Gingerich 1982, Gingerich and Rose 1982) and Unuchinia (Gunnell 1988) in the middle and late Paleocene, and the genus Apatemys (Gingerich and Rose 1982) in the Eocene. Jepsenella and Unuchinia are larger than Labidolemur and Apatemys. The I1 is from the Upper Level, and the p4's are from the Lower Level. These specimens are within the size range of Labidolemur. The p2 is from the Lower Level, and is within the size range of Jepsenella. This may indicate that there are two genera of Apatemyidae represented from the Hand Hills West, Lower Level, or that the p2 of the genera represented is not as reduced in size as the p2 in later genera (Labidolemur), or that there is interspecific variation in terms of size (juvenile/adult).

Order Lipotyphyla Haeckel 1816

Suborder Erinaceomorpha incertae sedis

Family Adapisoricidae Schlosser 1887

Subfamily Litocherinae Gingerich 1983

Genus Litocherus Gingerich 1983

Litocherus sp., cf. L. notissimus (Simpson 1936)

(Plate 2D; Table 25)

Holotype of Litocherus notissimus: AMNH 33831, left dentary with p2-m3, and associated left and right maxillae with C1-M3.

Type locality: Scarritt Quarry, Crazy Mountain Basin, Montana.

Known age and distribution of Litocherus notissimus: early Tiffanian of Montana (Type locality [Simpson 1936]).

Referred specimens: UALVP 35148, M1; 35258, LM2; 35110, 35112, M3s; 35113, left dentary fragment with p3-m1; 35119, 35115, 35116, 35122, 35124, 35192, m1s; 35130, m2.

Horizon: Hand Hills West, Upper Level and Lower Level.

Description:

The dentition of Litocherus notissimus has been adequately described and figured by Simpson (1937), Krishtalka (1973), and Gingerich (1983).

The upper molars and lower molars of L. zygeus are morphologically similar to L. notissimus, but differ in being smaller.

p3. - The protoconid is well developed and compressed labiolingually. The paraconid is small and cuspate, unlike that of L. zygeus (Gingerich 1983). The talonid is not basined, and there appears to have been a small cuspule on the entocristid.

p4. - The p4 of L. notissimus is smaller than that of L. zygeus, and more elongated. The protoconid is well developed, the metaconid is moderately developed and located posterior and lingual to the protoconid. The paraconid is distinct, as is the precingulum, and the talonid is short.

Discussion:

Litocherus notissimus is the smallest and oldest species of this genus, 18% smaller than L. zygeus, and 27% smaller than L. lacunatus (Gingerich 1983). Simpson (1936) described Litolestes notissimus from the early Tiffanian Scarrit Quarry in Montana and classified it as a hyopsodontid condylarth. Van Valen (1967) moved Litolestes to the Family Adapisoricidae (Lipotyphyla). Russell et al. (1975) retained this classification but suggested that this genus is closely related to condylarths. Gingerich (1983) moved Litolestes notissimus to the genus Litocherus, but retained it within the Family Adapisoricidae. The genus Litocherus is characterized by small, distinct stylar crests, prominent paracone and metacone, a small paraconid, and a more marked posterior molar reduction than Litolestes (Gingerich 1983). Litocherus differs from other Litocherinae in having a small premolariform p4.

Litocherus sp., cf. L. notissimus has been recovered from the middle Tiffanian of Alberta (UADW-2 locality, Paskapoo Formation, Blindman River [Fox 1990]; Joffre Bridge Roadcut locality, Paskapoo Formation, Red Deer River [Fox 1990]), and the late Tiffanian of Alberta (Police Point locality, Ravenscrag Formation, Cypress Hills [Krishtalka 1973]). This material is morphologically similar to that of Litocherus notissimus from the early Tiffanian of Montana, and is referred to Litocherus sp., cf. L. notissimus, to reflect its extended geological time range into the middle Tiffanian.

There is no significant difference between the samples from the Upper Level and Lower Level.

Litocherus sp., cf. L. zygeus Gingerich 1983

(Plate 2E, 2F; Table 26, 27)

Holotype of Litocherus zygeus: UM 64508, right dentary with p3-m3 intact.

Type locality: Cedar Point, Polecat Bench Formation, Bighorn Basin, Bighorn County, Wyoming.

Known age and distribution of Litocherus zygeus: Middle Tiffanian of Wyoming (Cedar Point, Polecat Bench Formation, Bighorn Basin, Bighorn County [Gingerich 1983]), North Dakota (Brisbane locality, Tongue River Formation, Grant County [Holtzman 1978]), and Alberta (UADW-2 locality, Paskapoo Formation, Blindman River [Fox 1990], Hand Hills West Upper Level, Paskapoo Formation [Fox 1990], Birchwood locality, Paskapoo Formation, Drayton Valley [M.W. Webb in prep.]); late Tiffanian (Judson locality, Tongue River Formation, Morton County [Holtzman 1978]).

Referred specimens: UALVP 35256, 35257, 35106, 35160, 35161, 35162, 35163, 35164, M2s; 35109, 35108, 35111, M3s; 35095, rp4-m2; 35114, 35169, left dentary fragments with p4-m2; 35174, 35097, right dentary fragments with m1-m2; 35171, 35089, 35090, 35091, 35092, 35093, 35094, p4s; 35069, 35166, 35167, 35172, 35176, 35074, 35073, 35194, 35195, 35196, 35206, 35211, 35098, 35104, 35105, 35134, 35132, 35133, 35125, 35118, 35098, 35099, 35045, 35100, 35103, 35215, 35128, 35101, 35102, 35103, m1s; 35135, 35136, 35131, 35123, 35126, 35127, 35129, 35117, 35120, 35121, 35168, 35170, 35173, 35178, 35181, 35182, 35183, 35173, 35174, 35122, m2s; 34923, 35150, 35151, 35177, 35179, 35183, 35096, 35152, 35165, m3s.

Horizon: Hand Hills West, Upper Level and Lower Level.

Description and discussion:

The dentition of *Litocherus zygeus* has been adequately described and figured by Gingerich (1983) and Holtzman (1978).

The specimens from the Hand Hills West, Upper Level and Lower Level, are identical in terms of size and morphology to that of *L. zygeus*, and are referred to *L.* sp., cf. *L. zygeus* to indicate the extended geological time range to the early Tiffanian (Ti2). The presence of *L. zygeus* from the Judson locality (Tongue River Formation, North Dakota [Holtzman 1978]) extends its geological time range to the late Tiffanian. The Judson locality is now considered to be late Tiffanian (Ti4) rather than middle Tiffanian (Ti3) in age (A.J. Kihm, pers. comm.).

There is a slight difference between the samples from the Upper Level and Lower Level. The talonid of the m3's from the Upper level is wider than the talonid of the m3's from the Lower Level.

Family Nyctitheriidae Simpson 1928

Genus *Leptacodon* Jepsen 1930

Leptacodon sp., cf. *L. packi* Jepsen 1930

(Plate 2G, 2H; Table 28)

Holotype of *Leptacodon packi*: Princeton University No. 13296, left lower jaw with p4-m3, and alveoli i2-p3.

Type locality: Princeton Quarry, Polecat Bench Formation, Big Sand Coulee, Park County, Wyoming.

Known age and distribution of *Leptacodon packi*: Middle Tiffanian (Late Paleocene) of Wyoming (Type locality [Jepsen 1930a], Cedar Point Quarry, Polecat Bench Formation, Bighorn Basin, Bighorn County [Rose 1981a]), and Alberta (UADW-2 locality, Paskapoo Formation, Blindman River [Fox 1990], Hand Hills West Upper Level, Paskapoo Formation [Fox 1990], Birchwood locality, Paskapoo Formation [Webb in prep. 1995]); late Tiffanian of Wyoming (Hoback Formation), and Alberta (Police Point locality, Ravenscrag Formation, Cypress Hills [Krishtalka 1973]).

Referred specimens: UALVP 35149, LM1-M2; 35145, 35147, 35269, 35270, M2s; 34929, rp2-m1; 35138, lp3-p4; 34927, rp4-m3; 34928, rp4-m3; 34932, 34931, rm2-m3; 34934, lm2-m3; 35143, 35140, 35141, 35144, 35209, 35139, p4s; 34924, 34938, 34935, 34937, 35137, 35204, 35207, 34930, 34935, m1s; 35208, 34936, m2s.

Horizon: Hand Hills West, Upper Level and Lower Level.

Description and discussion:

The upper molars and lower molars of Leptacodon packi have been adequately described and figured by Jepsen (1930a) and Krishtalka (1973). The lower premolars are not well known and are further described.

p2. - The distinctive features of this specimen are: (1) premolariform (the lingual side of this specimen is worn); (2) the protoconid is compressed labiolingually; and (3) the tip of the cusp is curved anteriorly.

p3. - The distinctive features of these specimens are: (1) the protoconid is straight and the tip is directed slightly posteriorly; (2) the paraconid is small, cuspate, oriented anteriorly, and set off on the precingulid; and (3) the talonid is poorly developed, with the labial side wider and sloped, and the lingual side forming a small shelf.

p4. - The distinctive features of these specimens are: (1) premolariform; (2) a well developed protoconid directed posteriorly; (3) the paraconid is connate and directed anteriorly; (4) the metaconid is moderately developed, connate, and is located posterolingually to the protoconid; and (5) the talonid is short, with the lingual portion forming a better developed shelf than in p3, and the labial portion is steeply sloped. The cristid obliqua and entocristid are better developed than in p3, and there appears to be a small cuspule on the cristid obliqua.

Discussion:

There is no significant difference between the samples from the Upper Level and Lower Level.

The presence of *Leptacodon* sp., cf. *L. packi* from the Hand Hills West, Lower Level, extends the geological time range to the early Tiffanian.

Leptacodon sp., cf. L. tener Matthew and Granger 1921

(Table 29)

Holotype of Leptacodon tener: AMNH 17179, lower jaws with badly crushed anterior part of skull.

Type locality: Mason Pocket, "Tiffany Beds", San Jose Formation, San Juan Basin, Colorado.

Known age and distribution of Leptacodon tener: Middle Tiffanian of Montana (Cedar Point Quarry, Polecat Bench Formation, Bighorn Basin, Bighorn County [Krishtalka 1976, Rose 1981]), Wyoming (Hoback Basin, Fort Union Formation), North Dakota (Brisbane locality, Tongue River Formation, Grant County [Holtzman 1978]; late Tiffanian of Colorado (type locality [Matthew and Granger 1921, McKenna 1968]), Alberta (Police Point locality, Ravenscrag Formation [Krishtalka 1973], Swan Hills site 1, Paskapoo Formation, Swan Hills [Stonley 1988]), and Saskatchewan (Roche Percée Local Fauna, Ravenscrag Formation [Fox 1990]).

Referred specimens: UALVP 35201, LM1; 35198, lm1.

Horizon: Hand Hills West, Lower Level.

Description:

M1. - UALVP 35201 represents the lingual part of an M1 from the base of the paracone and metacone. The protocone is directed anterolabially, the hypocone is distinct, and there is a small accessory cuspule on the precingulum. The upper molars of *L. tener* differ from *L. packi* in being more quadrate in occlusal view (Krishtalka 1973).

m1. - The lower molars have been adequately described and figured by McKenna (1968) and Krishtalka (1973). The lower molars of *L. tener* are morphologically identical to *L. packi* but are more narrow.

Discussion:

The presence of *Leptacodon* sp., cf. *L. tener* from the Hand Hills West, Upper Level, extends the geological time range to the early Tiffanian.

Genus Nyctitherium Marsh 1872

Nyctitherium sp.

(Plate 3A, 3B; Table 30)

Referred specimens: UALVP 34933, lm3; 34939, left dentary fragment with p2-p3.

Horizon: Hand Hills West, Upper Level.

Description:

UALVP 34939 is a left dentary fragment with p2-p3. The premolars are small and simple with a high laterally compressed protoconid, curved slightly posteriorly, increasing in size posteriorly. There is one mental foramen below the p3, which is characteristic of the genus Nyctitherium (Robinson 1968).

The premolars are morphologically similar to Nyctitherium serotinum (Robinson 1968) and Nyctitherium velox (Marsh 1872), but are smaller.

m3. - The distinctive features of UALVP 34933 are: (1) high, sharp cusps; (2) prominent paraconid, directed anteriorly and compressed labiolingually; (3) well-developed protoconid; (4) cuspate metaconid, approximately equal in height to the paraconid; (5) the pre- and postcingulid are well developed; (6) the hypoconid and hypoconulid are worn but appear to approximately equal in height; (7) the entoconid is the highest talonid cusp on a strong entocristid, and is smaller at the base than the other talonid cusps; and (8) the hypoconulid is centrally located and extended posteriorly.

The well-developed entoconid and strong entocristid are characteristic of the genus Nyctitherium (Robinson 1968, Krishtalka 1976).

UALVP 34933 differs from the m3 of N. velox (Robinson 1968) in being smaller, and the hypoconulid and entoconid not as closely appressed as in N. velox (Marsh 1872). This specimen differs from the m3 in N. serotinum in being smaller, and the presence of external cingulae (Robinson 1968).

Discussion:

Nyctitherium is known from the early Eocene of Colorado, and the early and middle Eocene of Wyoming and Utah (Robinson 1968, Krishtalka 1976).

Krishtalka (1973) referred material from the late Tiffanian Police Point locality to cf. Nyctitherium. Youzwyshyn (1988) referred material from the earliest Tiffanian Cochrane 2 locality to cf. Nyctitherium. The lower molars are characterized by the following features: (1) high, sharp cusps; (2) the protoconid and hypoconid are slanted posteriorly; (3) the paraconid is anteroposteriorly compressed, and medially located; (4) the hypoconulid and entoconid are appressed; (5) the entoconid is higher and larger than the hypoconulid; and (6) the pre- and postcingulum are well developed. Youzwyshyn (1988) noted that the primitive condition is morphologically identical to the m1 of Paranyctoides (Fox 1984d) from the late Cretaceous, the oldest and most primitive lipotyphylan.

Order Carnivora Bowdich 1821

Family Viverravidae Wortman and Matthew 1899

Genus Raphictis Gingerich and Winkler 1985

Raphictis sp., cf. R. gausion Gingerich and Winkler 1985

(Plate 3C-F)

Holotype of Raphictis gausion: PU 21244, left dentary with p3-m2.

Type locality: Cedar Point Quarry, Polecat Bench Formation, Bighorn Basin, Bighorn County, Wyoming.

Known age and distribution of Raphictis gausion: Middle Tiffanian (late Paleocene) of Wyoming (type locality [Gingerich and Winkler 1985]), and Alberta (Birchwood locality, Paskapoo Formation, Drayton Valley [M.W. Webb in prep.]).

Referred specimens: UALVP 35184, LM2; 35185.

Horizon: Hand Hills West Upper Level.

Description:

Undescribed material from the middle Tiffanian UADW-2 locality in Alberta and the late Tiffanian Roche Percée locality in Saskatchewan, has been referred to Raphictis sp., cf. R. gausion, including the previously unknown upper molars. This material is morphologically identical to teeth of Raphictis gausion from the Cedar Point Quarry, but is smaller. The M2 from the Hand Hills West Upper Level is described below.

M2. - The features of UALVP 35184 (L=2.4mm, W=3.8mm) are: (1) prominent paracone and protocone, the paracone being the highest cusp and directed slightly anteriorly; (2) well-developed parastylar shelf with a robust stylocone; (3) the paraconule is higher than the smaller but distinct metaconule; (4) the small postcingulum bears a small cuspule; (5) a strong preparacrista; and (6) the preparaconule crista forms a small shelf along the base of the paracone. The strongly developed stylocone, metacone, and metaconule represent the primitive condition, seen in Pristinictis connatus (Fox and Youzwyshyn 1994). This specimen differs from Pristinictis in the anteriorly directed paracone; in the M2 of Pristinictis the paracone is directed straight, and is narrower.

The lower molars of Raphictis gausion have been adequately described and figured by Gingerich and Winkler (1985) and Rose (1981).

m2. - UALVP 35185 is an isolated left lower second molar (L=2.7mm, AW=1.4mm, PW=1.1mm). The hypoconid and entoconid are reduced, which is characteristic of Raphictis (Gingerich and Winkler 1985). This specimen is morphologically identical to the m2 in Raphictis gausion from the middle Tiffanian Cedar Point Quarry (Gingerich and Winkler 1985) and Birchwood locality (Webb in prep.), but is slightly smaller.

Discussion:

Gingerich and Winkler (1985) noted that Pappictidops acies (Wang 1978) differed from the type species P. orientalis (Qiu and Li 1977), more closely resembling the type specimen of Raphictis in possessing narrower lower premolars and molars. They suggested that it could represent an Asian species of Raphictis.

Gingerich and Winkler (1985) suggested that Raphictis is derived from a species of Protictis that possessed a triangular P4 in occlusal view, reduced paraconid on m1, and a higher trigonid on m2.

4.0 RESULTS AND DISCUSSION

4.1 RELATIVE AGE OF THE LEVELS

The recovery of Plesiadapis rex and Ectocion cedrus from the Upper Level supports an age of middle Tiffanian (Ti3) for this level (Table 2). This zone extends from 61.2 to 58.3 million years ago (Sloan 1987). The faunal composition of the Upper Level in comparison to other middle Tiffanian localities in Alberta (Birchwood, UADW-2) suggests that it is geologically older than these localities, early middle Tiffanian in age (see discussion in 4.4 Faunal Comparison). The palynofloral results place the Lower Level within the P3 zone (Table 1), which ranges from the latest Torrejonian to the middle Tiffanian (Demchuk 1987, 1990). Magnetostratigraphic evidence indicates that this level is low within the 26r polarity zone (Table 1). This zone includes the early Tiffanian (Ti1 and Ti2) and the first part of the middle Tiffanian (Ti3), eliminating an age of latest Torrejonian. Therefore, the youngest this level could be is early Ti3 (approximately 58 million years), and the oldest it could be is Ti1 (62.3 million years) (Sloan 1987). The fact that the Lower Level was found low in the 26r zone supports an age of earliest Tiffanian (Ti1) or early Tiffanian (Ti2) (Lerbekmo et al. 1995). The faunal composition of the Lower Level is more similar to the Upper Level and other middle Tiffanian localities (UADW-2, Birchwood) than to the earliest Tiffanian Cochrane 2 locality (see discussion in 4.4 Faunal Comparison). Therefore, the Lower Level is likely early Tiffanian (Ti2) in age. This zone extends from 61.8 to 61.2 million years ago (Sloan 1987).

Estimates of sedimentation rates for the late Paleocene vary dramatically (e.g., 0.200m/1000y for the Hoback Basin versus 0.100/1000y for the Bighorn Basin [Schwab 1976]), as do the methods used for the measurements of these rates (e.g., the assumption of continuous sedimentation, the use of mean as opposed to minimum accumulation rates, and long term versus short term rates) (Tipper 1983, Sadler 1981, Anders et al. 1987). Based on the sedimentation rate for the Paskapoo Formation, 0.075m/1000y (Lerbekmo et al. 1995), the amount of time represented between the Upper Level and Lower Level (22 metres) is a minimum of 293,000 years. The disconformity between the Upper Level and Lower Level (see discussion in 1.1 Location) precludes determining the precise amount of time between the two levels.

4.2 GEOLOGICAL TIME RANGES

Earliest Tiffanian (Ti1) and middle Tiffanian (Ti3) mammals are relatively well known in western Canada. The Hand Hills West Lower Level represents the only known locality outside of Montana, that is early Tiffanian (Ti2) in age. The relatively short period of time between the Upper Level and the Lower Level and their stratigraphic superpositional relationship, provides the opportunity to extend the geological time ranges of earliest Tiffanian and middle Tiffanian species into younger and older zones, respectively (Table 31). Fossils recovered from the Lower Level extend the geological time range of the plesiadapiform primate Elphidotarsius wightoni into older sediments. The Upper Level extends the geological time range of the plesiadapiform primate

Nannodectes gidleyi into older sediments, and the pentacodontid Bisonalveus sp., cf. B. browni and the multituberculate Baiotomeus into younger sediments.

4.3 FAUNAL COMPOSITION

The overall abundance and distribution of taxa from the Upper Level and Lower Level of the Hand Hills West locality are similar (Table 32, Figures 2 and 3). The temporal distance between these two levels is relatively small (minimum approximately 300,000 years). The observed differences between the two horizons are primarily indicative of taphonomic and sampling bias. More subtle differences may be due to evolutionary change. For example, there are differences in size and morphology of the dentitions of Carpodaptes and Litocherus between the Upper Level and Lower Level. The significance of these differences is not clear, as the distributions of these characteristics do not follow a consistent stratigraphic pattern with other Tiffanian localities.

Sources of Bias -

Sample sizes (of identifiable specimens) from the Upper and Lower levels are 252 and 113 respectively. Taxa that are unknown from the Lower Level (e.g., Peradectes, Saxonella) have very few representatives in the Upper Level. Therefore, as the sample size is reduced, the likelihood of finding these taxa is decreased proportionately.

In general, taxa of larger body size (e.g., condylarths) are absent from the two assemblages. Smaller specimens (<3mm) are typically well preserved, being complete to nearly complete with little wear. Moderately-sized specimens (3mm - 6mm) are often well worn and somewhat fragmentary. Specimens from larger mammals (e.g., Ectocion) are rare, extremely worn, and severely fragmented.

Taphonomic differences may also account of the apparent infrequency and/or absence in the Lower Level of taxa that attained moderate body size, such as plesiadapiform primates in the Lower Level. Overall, the specimens from the Lower Level tend to be more fragmentary and worn than those from the Upper Level. The scarcity of specimens of condylarths from both levels and of plesiadapid primates from the Lower Level is likely due to a preservational bias towards smaller material, rather than being reflective of the actual abundance of these groups at the time.

This preservational bias towards smaller specimens is due in part to the depositional environment. The Upper Level likely represents a channel fill deposit and the Lower Level may represent a floodplain deposit. The texture of both deposits indicate continued accumulation of fine-grained sediments in a relatively quiet depositional environment, which creates a bias towards smaller specimens (Behrensmeyer 1982, 1988). The differential preservation and abrasion among differently sized specimens supports the transport of this material over relatively long distances and a relatively long period of time, which is characteristic of these types of fluvial deposits (Behrensmeyer 1982, 1988).

Based on the relative abundance and distribution of taxa recovered, small lipotyphylans and "insectivorans" (e.g., Litocherus and Leptacodon) are the most abundant, moderately sized primates are moderately abundant, and multituberculates are relatively uncommon (Table 32, Figures 2 and 3). The abundance of small mammals may in part be due to the depositional environment and taphonomic bias, but they likely represented a dominant part of the faunal assemblage as in other Tiffanian localities in western Canada (Fox 1990).

Faunal completeness -

Sampling bias and differential preservation can result in the faunal richness being underestimated. Maas and Krause (1994) used an index of relative generic completeness to correct for this bias in richness estimates (see Appendix). This index assumes that if a taxon is known before or after an interval, its absence is due to sampling bias (Maas and Krause 1994, Maas et al. 1995). Maas et al. (1995) considered a completeness index of less than 70 for an interval, which indicates that more than 30% of the estimated number of genera are unknown from an interval, as not adequately sampled. The completeness indices for western Canada indicate that the early Tiffanian (Ti2) and late Tiffanian (Ti4) are not adequately sampled (Table 37). These intervals, Ti2 and Ti4, are also not adequately sampled for the Big Horn Basin and Crazy Mountain Basin (Table 38).

4.4 FAUNAL COMPARISON

The precise definition of species diversity and how to measure it has been the subject of much discussion (Peet 1974, Whittaker 1977). Species diversity is the result of several factors, including area effect, spatial heterogeneity, climate stability and predictability, and stability of food resources (Krause and Maas 1990). Species diversity is often used as a dual concept of species richness and species equatability or evenness. Species richness is based on the number of species in an assemblage and is considered to be the primary measure of diversity. Species equatability or evenness is based on the relative abundance of species. The measure of heterogeneity is the combination of species richness and evenness, and is a measure of uncertainty in the faunal assemblage.

There are four indices usually used for the comparison of extinct faunal assemblages, two measures of species evenness and two measures of heterogeneity (see Appendix). Whittaker's Index (1972, 1977) and Pielou's Index (1966) measure species evenness (a decrease in the index reflects a decline in evenness). The Shannon-Wiener Index (Peet 1974) is a measure of heterogeneity. It is considered to be more sensitive to abundances of rarer species than other indices (Rose 1981b). Simpson's Index (1949) is also a measure of heterogeneity. It measures the probability that two individuals selected at random will be from the same species, and reflects proportional abundances. It is usually calculated as 1-L (L being Simpson's Index) so that an increase in the index reflects an increase in heterogeneity (Rose 1981b). It is strongly affected by the abundance of the most common species, and it reflects concentrations of dominant species (Rose 1981b).

Upper Level and Lower Level

The Pielou, Shannon-Weiner, and Simpson indices are similar for the Upper Level and Lower Level (Table 36). Whittaker's Index differs dramatically between the Upper Level and Lower Level. The middle Tiffanian Brisbane locality of North Dakota (Table 36) also has an unusually high Whittaker's Index, compared to other middle Tiffanian localities in Wyoming and western Canada. Rose (1981b) suggested that the small sample size, and the absence of larger mammals from the fauna, due to a taphonomic bias towards small mammals, results in an apparent low species diversity and therefore a high species evenness. The Lower Level also has a small sample size, and a taphonomic bias towards small mammals. This may account for the disparity in the Whittaker's Index between the Upper Level and Lower Level. The Pielou Index, which is also considered to measure species evenness, is identical for both the Upper Level and Lower Level.

Lower Level and Scarritt Quarry

The Hand Hills West Lower Level and the Scarritt Quarry locality (Montana) are the only known localities that are Ti2 in age. Scarritt Quarry is characterized as having a relatively low species richness and evenness (Rose 1981a). The uncommon occurrence of the plesiadapiform primate Plesiadapis, the multituberculate Ptilodus, the absence of phenacodontid condylarths and carnivorans, and the low diversity, were believed to be the result of size sorting (most of the sample is represented by small mammals) and small sample size (Rose 1981a). Further sampling has recovered more plesiadapiform primates and multituberculates, and the following groups previously not known from Scarritt Quarry, dermopterans, condylarths, pantodonts and carnivorans (Krause and Maas 1994). Unfortunately, species richness and evenness indices based on the subsequent samples are not available for comparison. Based on the indices from earlier samples (Rose 1981a), Scarritt Quarry has a lower species diversity and species richness than the Lower Level (Table 36). More recent faunal lists (Table 33) indicate a similar faunal composition.

It is interesting to note that the faunal relationship between the early Tiffanian (Ti2) Scarritt Quarry locality in Montana and the middle Tiffanian (Ti3) Cedar Point locality in Wyoming is similar to that of the Upper Level and Lower Level. Rose (1981b) characterized the faunal assemblage of Scarritt Quarry as very similar to, but slightly more primitive than, that of Cedar Point. The Lower Level is characterized by slightly more primitive species than the Upper Level. In both the Scarritt Quarry - Cedar Point comparison and the Upper Level - Lower Level comparison, the Pielou Index is identical, and the Simpson and Shannon-Weiner indices are slightly higher for the younger localities (Table 36).

Upper Level and other middle Tiffanian localities

The Hand Hills West Upper Level differs from other middle Tiffanian localities in Alberta primarily in the absence of several condylarths and of pantodonts (Table 34). This is likely due to taphonomic differences. In the Upper Level, as in the Lower Level, specimens of small mammals are abundant and relatively well preserved, and larger mammals are usually fragmentary and poorly preserved. The faunal composition of other middle Tiffanian localities in Alberta appears more similar to each other, and late Tiffanian localities, than to the Upper Level (Table 34). For example, an undescribed new species of Bisonalveus (Bisonalveus "gracilis", M.W. Webb in prep.) has been recovered from the UADW-2 and Birchwood localities. Bisonalveus browni is considered to be more primitive and has been recovered from the earliest Tiffanian Cochrane 2 locality, and the Hand Hills West, Upper Level and Lower Level. In addition, genera that are known from the middle Tiffanian (Ti3) and the late Tiffanian (Ti4) are found in the UADW-2 and Birchwood localities, and not the Hand Hills West, Upper Level (Table 35). These genera include the carnivoran Protictis, the multituberculate Microcosmodon, and the condylarth Cyriacotherium. The faunal comparison indicates that the Upper Level may be older than these localities, early middle Tiffanian in age.

4.5 FAUNAL TURNOVER

Rose (1981b) reviewed the faunal composition and relative diversity of late Paleocene and early Eocene mammal-bearing localities in North America, and noted that the Torrejonian (middle Paleocene) and Wasatchian (early Eocene) appeared to be characterized by a higher species diversity than the Tiffanian (late Paleocene) and Clarkforkian (latest Paleocene). Rose (1981b) indicated that the late Torrejonian Douglass Quarry (Montana) is characterized by a much higher species richness (diversity) and equitability (evenness) than the Tiffanian Cedar Point (Wyoming) and Scarritt Quarry (Montana) localities. Based on this, Rose (1981b) suggested that the pattern of species diversity indicated that the Torrejonian and Wasatchian were times of environmental stability, and the Tiffanian and Clarkforkian were times of environmental instability, and that this was reflected in an actual drop in species diversity.

Youzwyshyn (1988) described the mammalian fauna from the earliest Tiffanian Cochrane 2 locality (Alberta), and found it to be far more species rich and diverse than other earliest Tiffanian localities. Youzwyshyn (1988) suggested that the difference was due in part to sample size, and the method of preparation, but that late Torrejonian localities had been extensively quarried, and that these results reflected an increased diversity in the early Tiffanian. This high diversity was unexpected according to Rose's (1981b) hypothesis, which suggested a higher diversity in the late Torrejonian and a decline in the early Tiffanian.

Maas et al. (1995) recognized four intervals of faunal change in the late Paleocene and early Eocene of the Bighorn and Crazy Mountain Basins (Wyoming and Montana). These intervals are based on changes in standing generic richness (Nsr), which estimates the generic richness at the midpoint of an interval (see Appendix). The late Torrejonian to the early Tiffanian was characterized by a decrease in generic richness, with a high rate of last occurrences. The late Tiffanian indicated an increased generic richness, with a high rate of first occurrences. There was an increase in generic richness in the earliest Wasatchian, with a high rate of first occurrences, and a decrease in the middle and late Wasatchian. Maas et. al (1995) suggested that the increased generic diversity in the late Tiffanian and the early Wasatchian was due to the immigration of taxa from other continents, in the former, and global warming and the open high latitude intercontinental dispersal routes at the Paleocene-Eocene boundary in the latter.

Contrary to Rose's (1981b) hypothesis, the faunal turnover of the early and middle Tiffanian is not significant, and the late Torrejonian and early Tiffanian represent ecological stability, with no significant change in ordinal level, despite the drop in generic richness (Maas et al. 1995). According to Maas et al. (1995), the drop in generic richness in the late Torrejonian and early Tiffanian is likely due to endemic anagenesis and cladogenesis. This does not account for the unusually high generic and species diversity in the earliest Tiffanian of Alberta (Youzwyshyn 1988). Krause and Maas (1990) suggest that the low rate of first occurrences in the early Tiffanian (Ti2), and the high rate of first occurrences in the middle Tiffanian (Ti3) are due to sampling bias, and that the Tiffanian is represented by a steady generic richness (Table 38).

The late Paleocene (Tiffanian) mammalian fauna of western Canada is relatively well represented. The standing generic richness for mammals through the Tiffanian of western Canada remains relatively stable, and is comparable to that seen in Montana and Wyoming (Table 37, 38). Latest Torrejonian and latest Tiffanian (Ti5) localities are not known from western Canada, and early Tiffanian (Ti2) and late Tiffanian (Ti4) localities are poorly sampled (Table 37). Although the generic richness of Tiffanian localities in Wyoming and Montana and those in western Canada are similar (with the exception of the earliest Tiffanian), the species richness is notably higher in the latter (Table 37, 38).

Tiffanian localities in Alberta often have considerably smaller sample sizes than localities in North Dakota, Montana and Wyoming, yet in many cases have a higher species diversity (Table 37, 38). It is likely that comparable samples sizes in western Canada would yield an even higher species diversity in the early and middle Tiffanian.

5.0 CONCLUSIONS

The Hand Hills West locality consists of two fossiliferous layers in superposition and represents consecutive intervals of the early (Ti2) and middle (Ti3) Tiffanian. The faunal composition between the two levels is similar and the differences observed are due primarily to taphonomic and sampling bias. The faunal assemblages extend the geological time ranges of several plesiadapiform primates, a pentacodontid, and a genus of multituberculate.

Faunal turnover patterns indicate a relatively stable generic richness among mammals in the late Paleocene of North America. The generic richness of Tiffanian localities in western Canada does not differ significantly from those of the United States. The higher species diversity in western Canada is of interest, but the significance of this difference is not clear. Several intervals of the late Paleocene from western Canada have yet to be recovered or are poorly sampled (e.g., latest Torrejonian, latest Tiffanian). Further samples are necessary to determine the generic richness throughout the Paleocene of western Canada, and the patterns in faunal turnover. The importance of this region as one of the primary routes of intercontinental exchange lends itself to questions of faunal changes and faunal turnover patterns.

Formation	[1] Palynofloral Zone	[2] Land Mammal Age	Zone	[3] Polarity Zone
Paskapoo	P6	Clarkforkian	Cl1	25 ■
		56.2		
	P5	Tiffanian	Ti5	25r
			Ti4	26 ■
	P4		Ti3	
	P3		Ti2	26r
			Ti1	
		62.3		
Scollard		Torrejonian	To3	27 ■
	P2		To2	27r
			To1	28 ■
		65.4		28r
		Puercan	Pu2	
	P1		Pu1	29 ■
		66.5		
	K	Lancian	La3	29r

Table 1 Palynofloral and magnetostratigraphic zonation of the early and middle Paleocene.

[1] Palynofloral zones taken from Demchuk (1987, 1990).

[2] Dates for North American Land Mammal Age Zones taken from Rose (1981).

[3] Magnetostratigraphic zones taken from Lerbekmo et. al. (1995).

Land Mammal Age	Zone	Biostratigraphic Zone (Gingerich, 1975)	Biostratigraphic Zone (Thewissen, 1990)		Hand Hills West	[1] Localities Montana, Wyoming, North Dakota	[2] Localities (Alberta)
Clarkforkian	Cl1	*Plesiadapis gingerichi*	*Ectocion major* *E. osbornianus*				
56.2							
Tiffanian	Ti5	*Plesiadapis simsoni*	*Ectocion cedrus*	*E. mediotuber*			
	Ti4	*Plesiadapis churchilli*					
	Ti3	*Plesiadapis rex*		*Ectocion collinus*	Upper Level	[3]Cedar Point [4]Judson [4]Brisbane	[5]Blindman River [6]Birchwood
	Ti2	*Plesiadapis anceps*			Lower Level	[3]Scarrit Q.	
	Ti1	*Plesiadapis praecursor*					[7]Cochrane
62.3							
Torrejonian	To3	*Pronothodectes jepi*	*Tetraclaenodon puercensis*				

Table 2 Biostratigraphic zonation and associated localities of the Tiffanian. Localities are list in alphabetical order and do not reflect stratigraphic sequence within the zone. Time ranges were taken from Sloan, 1987.

[1] Localities representing the late Torrejonian, latest Tiffanian and Clarkforkian are discussed in Rose, 1981.
[2] Localities representing the late Torrejonian and latest Tiffanian are discussed in Fox, 1990.
[3] Rose, 1981. [4] Holtzman, 1978. [5] Fox, 1990. [6] Webb, In prep. [7] Youzwyshyn, 1988.

Table 3 Measurements and descriptive statistics the dentition of Mimetodon silberlingi from the Hand Hills West locality, Upper Level and Lower Level.

P	OR		Mean	N	SD	CV
p4	L=	2.7	2.7	1	-	-
	W=	0.9-1.1	1.0	4	0.1	0.05
	H=	1.6-2.1	1.9	4	0.3	0.5
M2	L=	1.0	1.0	1	-	-
	W=	1.1	1.1	1	-	-

Table 4 Measurements and descriptive statistics of the dentition of Mesodma pygmaea from the Hand Hills West locality, Upper Level and Lower Level.

P	OR		Mean	N	SD	CV
M2	L=	0.8-1.0	0.9	3	0.1	0.06
	W=	0.9-1.0	0.8	4	0.2	0.1
p4	L=	2.8	2.8	1	-	-
	W=	1.0	1.0	1	-	-
	H=	2.2	2.2	1	-	-
m1	L=	1.8	1.8	2	-	-
	W=	0.7-0.8	0.8	2	0.1	0.07
m2	L=	1.0	1.0	1	-	-
	W=	0.9	0.9	1	-	-

Table 5 Measurements and descriptive statistics of the dentition of Neoplagiaulax sp., cf. N. hazeni from the Hand Hills West locality, Upper Level and Lower Level.

P	OR		Mean	N	SD	CV
P4	L=	3.0-3.2	3.1	3	0.15	0.09
	W=	1.2-1.3	1.3	3	0.05	0.03
M1	L=	-	-	-	-	-
	W=	1.4	1.4	1	-	-
M2	L=	1.4-1.6	1.5	3	0.1	0.06
	W=	1.4-1.5	1.5	3	0.1	0.06
p4	L=	4.9	4.9	1	-	-
	W=	1.5	1.5	1	-	-
	H=	-	-	-	-	-
m1	L=	2.3-2.6	2.5	5	0.13	0.06
	W=	1.0-1.2	1.1	6	0.04	0.02
m2	L=	1.7	1.7	1	-	-
	W=	1.3	1.3	1	-	-

Table 6 Measurements and descriptive statistics of the dentition of *Neoplagiaulax hunteri* from the Hand Hills West locality, Upper Level and Lower Level.

P	OR		Mean	N	SD	CV
P4	L=	3.1	3.1	1	-	-
	W=	1.2	1.2	1	-	-
M1	L=	3.4	3.4	1	-	-
	W=	1.5	1.5	1	-	-
M2	L=	1.4	1.4	2	-	-
	W=	1.4-1.5	1.5	2	0.1	0.07
p4	L=	-	-	-	-	-
	W=	1.3	1.3	2		
	H=	3.5	3.5	1	-	-
m1	L=	2.4-2.6	2.5	2	0.2	0.14
	W=	1.1-1.2	1.2	2	0.1	0.07
m2	L=	1.5	1.5	1	-	-
	W=	1.2	1.2	1	-	-

Table 7 Measurements and descriptive statistics of the dentition of *Neoplagiaulax sp.* from the Hand Hills West locality, Upper Level and Lower Level.

P	OR		Mean	N	SD	CV
M1	L=	2.6-3.4	3.0	4	0.3	0.13
	W=	1.2-1.5	1.4	4	0.17	0.08
p4	L=	4.5-5.1	4.7	3	0.4	0.2
	W=	1.2-1.6	1.4	3	0.2	0.12
	H=	3.0-4.0	3.5	3	0.6	0.4

Table 8 Measurements and descriptive statistics of the dentition of Ptilodus sp. C from the Hand Hills West locality, Upper Level.

P	OR		Mean	N	SD	CV
P1	L=	2.5-2.6	2.6	2	0.1	0.07
	W=	2.6-3.2	2.9	2	0.6	0.4
P2	L=	2.7-3.2	3.0	2	0.5	0.4
	W=	2.2-2.8	2.5	2	0.6	0.4
P3	L=	2.8	2.8	1	-	-
	W=	2.2	2.2	1	-	-
P4	L=	6.0	6.0	1	-	-
	W=	2.6	2.6	1	-	-
M1	L=	3.6-4.1	3.9	2	0.5	0.4
	W=	1.8	1.8	2	-	-
M2	L=	2.6	2.6	1	-	-
	W=	2.1	2.1	1	-	-
m1	L=	4.1	4.1	1	-	-
	W=	2.1	2.1	1	-	-

Table 9 Measurements and descriptive statistics of the dentition of *Peradectes* *elgans* from the Hand Hills West locality, Upper Level.

P	OR		Mean	N	SD	CV
M1	L=	1.4	1.4	1	-	-
	W=	1.2	1.2	1	-	-
M3	L=	1.7-1.9	1.8	2	1.1	0.8
	W=	1.5-1.6	1.6	2	0.1	0.07
m1	L=	2.7	2.7	1	-	-
	W=	1.6	1.6	1	-	-
m2	L=	2.2	2.2	1	-	-
	AW=	1.5	1.5	1	-	-
	PW=	1.5	1.5	1	-	-
m3	L=	1.6	1.6	1	-	-
	AW=	1.6	1.6	1	-	-
	PW=	1.6	1.6	1	-	-

Table 10 Measurements and descriptive statistics of the dentition of *Peradectes* sp. from the Hand Hills West locality, Upper Level.

P	OR		Mean	N	SD	CV
M3	L=	1.6	1.6	1	-	-
	W=	1.3	1.3	1	-	-
m2	L=	1.2	1.2	1	-	-
	AW=	0.9	0.9	1	-	-
	PW=	0.9	0.9	1	-	-

Table 11 Measurements and descriptive statistics of the dentition of Elphidotarsius wightoni from the Hand Hills West locality, Upper Level and Lower Level.

P	OR		Mean	N	SD	CV
P4	L=	1.5	1.5	1	-	-
	W=	-	-	-	-	-
M1	L=	1.6	1.6	1	-	-
	W=	2.2	2.2	1	-	-
M2	L=	1.5	1.5	1	-	-
	W=	2.3	2.3	1	-	-
M3	L=	1.3	1.3	1	-	-
	W=	2.2	2.2	1	-	-
i1	L=	1.5	1.5	1	-	-
	W=	0.8	0.8	1	-	-
	H=	1.9	1.9	1	-	-
p4	L=	1.8-1.9	1.9	2	0.1	0.07
	W=	1.0-1.1	1.1	2	0.1	0.07
m2	L=	1.1	1.1	2	-	-
	AW=	0.8-0.9	0.9	2	0.1	0.07
	PW=	1.0-1.1	1.1	2	0.1	0.07
m3	L=	1.6-2.2	1.8	3	0.4	0.2
	AW=	0.8-1.2	1.0	3	0.2	0.12
	PW=	1.0-1.2	1.1	3	0.1	0.06

Table 12 Measurements and descriptive statistics of the dentition of Elphidotarsius russelli from the Hand Hills West locality, Lower Level.

P	OR		Mean	N	SD	CV
I1	L=	1.5	1.5	1	-	-
	W=	0.8	0.8	1	-	-
	H=	3.3	3.3	1	-	-
P3	L=	1.6	1.6	1	-	-
	W=	-	-	-	-	-

Table 13 Measurements and descriptive statistics of the dentition of *Carpodaptes hazelae* from the Hand Hills West locality, Upper Level

P	OR		Mean	N	SD	CV
P3	L=	1.8	1.8	1	-	-
	W=	1.9	1.9	1	-	-
M2	L=	1.3	1.3	1	-	-
	W=	1.9	1.9	1	-	-
p4	L=	2.1-2.4	2.3	3	0.2	0.12
	W=	1.3-1.6	1.5	3	0.2	0.12
m2	L=	1.4-1.5	1.5	2	0.1	0.07
	AW=	1.0	1.0	2	-	-
	PW=	1.2	1.2	2	-	-
m3	L=	1.9	1.9	1	-	-
	AW=	1.1	1.1	1	-	-
	PW=	1.2	1.2	1	-	-

Table 14 Measurements and descriptive statistics of the dentition of *Carpodaptes* sp., cf. *C*. *hazelae* from the Hand Hills West locality, Lower Level.

P	OR		Mean	N	SD	CV
P4	L=	1.6-2.3	1.9	3	0.5	0.3
	W=	1.8-2.9	2.5	3	0.7	0.4
M1	L=	1.3	1.3	2	-	-
	W=	2.4-2.5	2.5	2	0.1	0.07
M3	L=	1.1	1.1	1	-	-
	W=	2.5	2.5	1	-	-
c	L=	1.1	1.1	1	-	-
	W=	0.6	0.6	1	-	-
p4	L=	2.4-2.6	2.5	2	0.2	0.14
	W=	1.3-1.8	1.6	2	0.5	0.4
m1	L=	1.5	1.5	2	-	-
	AW=	1.1-1.4	1.3	2	0.3	0.2
	PW=	1.1-1.2	1.2	2	0.1	0.07
m2	L=	1.2-1.3	1.3	4	0.07	0.04
	AW=	0.7-0.9	0.8	4	0.07	0.04
	PW=	1.1-1.2	1.1	4	0.03	0.02
m3	L=	1.9	1.9	1	-	-
	AW=	0.8	0.8	1	-	-
	PW=	1.1	1.1	1	-	-

Table 15 Measurements and descriptive statistics of the dentition of *Plesiadapis rex* from the Hand Hills West locality, Upper Level.

P	OR		Mean	N	SD	CV
P4	L=	2.1	2.1	2	-	-
	W=	3.0-3.1	3.1	2	0.1	0.07
p4	L=	2.7	2.7	1	-	-
	W=	1.9	1.9	1	-	-
m2	L=	3.1	3.1	1	-	-
	AW=	2.6	2.6	1	-	-
	PW=	-	-	-	-	-

Table 16 Measurements and descriptive statistics of the dentition of Nannodectes simpsoni from the Hand Hills West locality, Upper Level.

P	OR		Mean	N	SD	CV
M2	L=	2.3	2.3	1	-	-
	W=	4.2	4.2	1	-	-
M3	L=	2.6	2.6	1	-	-
	W=	3.6	3.6	1	-	-
i1	L=	3.5	3.5	2	-	-
	W=	2.0	2.0	2	-	-
	H=	7.1	7.1	1	-	-
p3	L=	1.8	1.8	1	-	-
	W=	1.2	1.2	1	-	-
p4	L=	1.7-2.1	1.9	2	0.4	0.3
	W=	1.8	1.8	2	-	-

Table 17 Measurements and descriptive statistics of the dentition of Ignacius frugivorus from the Hand Hills West locality, Upper Level and Lower Level.

P	OR		Mean	N	SD	CV
I1	L=	1.2	1.2	1	-	-
	W=	1.3	1.3	1	-	-
	H=	2.9	2.9	1	-	-
P4	L=	1.9	1.9	1	-	-
	W=	2.0	2.0	1	-	-
M1	L=	1.7	1.7	1	-	-
	W=	2.6	2.6	1	-	-
M2	L=	1.9	1.9	1	-	-
	W=	2.4	2.4	1	-	-
M3	L=	1.7	1.7	1	-	-
	W=	2.4	2.4	1	-	-
m2	L=	1.5-1.8	1.7	2	0.3	0.2
	AW=	1.2-1.4	1.3	2	0.2	0.1
	PW=	1.2-1.3	1.3	2	0.1	0.07
m3	L=	2.6	2.6	1	-	-
	AW=	1.3	1.3	1	-	-
	PW=	1.3	1.3	1	-	-

Table 18 Measurements and descriptive statistics of the dentition of Ectocion cedrus from the Hand Hills West locality, Upper Level.

P	OR	Mean	N	SD	CV
DP3	L= 4.7	4.7	1	-	-
	W= 3.7	3.7	1	-	-
P3	L= 4.7-5.3	5.0	3	0.4	0.2
	W= 4.4-5.0	4.8	3	0.4	0.2
M1	L= 6.0-6.5	6.3	2	0.5	0.4
	W= 8.5-8.8	8.7	2	0.3	0.2
M2	L= 6.3-6.5	6.4	2	0.2	0.1
	W= 8.8	8.8	1	-	-
M3	L= 5.4	5.4	1	-	-
	W= 7.2	7.2	1	-	-
p3	L= 5.3	5.2	1	-	-
	W= 3.6	3.6	1	-	-
p4	L= 5.7-6.3	6.0	2	0.6	0.4
	W= 4.2	4.2	1	-	-
dp4	L= 5.7	5.7	1	-	-
	W= 3.7	3.7	1	-	-
m2	L= 6.0	6.0	1	-	-
	AW= 4.7	4.7	1	-	-
	PW= 4.7	4.7	1	-	-
m3	L= 6.4	6.4	1	-	-
	AW= 4.3	4.3	1	-	-
	PW= 3.4	3.4	1	-	-

Table 19 Measurements and descriptive statistics of the dentition of Elpidophorus elegans from the Hand Hills West locality, Upper Level and Lower Level.

P	OR		Mean	N	SD	CV
DP2	L=	3.9	3.9	1	-	-
	W=	3.2	3.2	1	-	-
M1	L=	3.4-3.9	3.7	2	0.5	0.4
	W=	5.3-5.4	5.4	2	0.1	0.07
M2	L=	5.4	5.4	1	-	-
	W=	3.8	3.8	1	-	-
i1	L=	-	-	1	-	-
	W=	-	-	1	-	-
p1	L=	1.9-2.0	1.9	2	0.1	0.07
	W=	1.1-1.3	1.2	2	0.2	0.1
p3	L=	2.8	2.8	1	-	-
	W=	1.9	1.9	1	-	-
dp3	L=	2.2-2.4	2.3	2	0.2	0.1
	W=	1.1-1.5	1.3	2	0.4	0.3
p4	L=	3.6	3.6	1	-	-
	W=	2.5	2.5	1	-	-
m2	L=	3.4	3.4	1	-	-
	AW=	2.6	2.6	1	-	-
	PW=	2.9	2.9	1	-	-

Table 20 Measurements and descriptive statistics of the dentition of Order Incertae Sedis from the Hand Hills West locality, Lower Level.

P	OR		Mean	N	SD	CV
I1	L=	1.0-1.3	1.1	4	0.2	0.08
	W=	1.1-1.4	1.2	4	0.2	0.08
	H=	1.9-2.4	2.1	3	0.3	0.1

Table 21 Measurements and descriptive statistics of the dentition of *Propalaeosinopa septenrionalis* from the Hand Hills West locality, Upper Level and Lower Level.

P	OR		Mean	N	SD	CV
M1	L=	2.3-2.6	2.4	3	0.2	0.09
	W=	3.0-3.6	3.3	4	0.3	0.1
M2	L=	2.6	2.6	1	-	-
	W=	2.8	2.8	1	-	-
M3	L=	2.5	2.5	1	-	-
	W=	3.8	3.8	1	-	-
m3	L=	2.2-2.3	2.3	2	0.1	0.07
	AW=	1.1-1.3	1.2	2	0.2	0.1
	PW=	1.2-1.4	1.3	2	0.2	0.1

Table 22 Measurements and descriptive statistics of Pararyctes pattersoni from the Hand Hills West locality, Upper Level and Lower Level.

P	OR	Mean	N	SD	CV
M1	L= 1.9	1.9	1	-	-
	W= 2.8	1.8	1	-	-
dp4	L= 2.3	2.3	1	-	-
	W= 1.3	1.3	1	-	-
p5	L= 2.0	2.0	1	-	-
	W= -	-	-	-	-
m1	L= 2.1-2.2	2.2	2	0.1	0.07
	AW= 1.3-1.8	1.6	3	0.3	0.18
	PW= 1.0-1.5	1.3	2	0.5	0.36
m2	L= 2.0-2.1	2.0	7	0.05	0.02
	AW= 1.5-1.9	1.7	7	0.13	0.05
	PW= 1.2-1.4	1.3	6	0.06	0.03
m3	L= 1.96-2.0	2.0	2	0.04	0.03
	AW= 1.6-1.7	1.7	2	0.05	0.03
	PW= 0.91-1.2	1.1	2	0.1	0.07

Table 23 Measurements and descriptive statistics of species of the dentition of Pararyctes from the Hand Hills West locality, Upper Level and Lower Level, and Pararyctes rutherfordi (Youzwyshyn 1988).

	P. pattersoni		*Pararyctes* sp.2		*Pararcytes* sp.1		*Pararyctes* sp.		*P. rutherfordi*	
P	OR	X	OR	X	OR	X	OR	X	OR	X
M1	L= 1.9 W= 2.8	1.9 2.8	-	-	-	-	-	-	-	-
M2	-	-	-	-	-	-	L= 4.3 W= 7.0	4.3 7.0	L= 2.8 W= 4.7	2.8 4.7
dp4	L= 2.3 W= 1.3	2.3 1.3	-	-	-	-	-	-	-	-
p5	L= 2.0 W=	2.0	-	-	-	-	-	-	-	-
m1	L= 2.1-2.2 AW= 1.3-1.8 PW= 1.0-1.5	2.2 1.6 1.3	-	-	-	-	-	-	L= 2.8 AW= 1.8-2.3 PW= 2.3	2.8 2.1 2.3
m2	L= 2.0-2.1 AW= 1.5-1.9 PW= 1.2-1.4	2.0 1.7 1.3	L= 2.7 AW= 2.0 PW= 1.9	2.7 2.0 1.9	L= 1.7 AW= 1.5 PW= 1.3	1.7 1.5 1.3	-	-	-	-
m3	L= 1.96-2.0 AW= 1.6-1.7 PW= 0.91-1.2	2.0 1.7 1.1	L= 2.8 AW= 1.8 PW= 1.5	2.8 1.8 1.5	L= - AW= 1.1 PW= -	- 1.1 -	-	-	-	-

Table 24 Measurements and descriptive statistics of the dentition of *Bisonalveus* sp., cf. *B. browni* from the Hand Hills West locality, Upper Level and Lower Level.

P	OR	Mean	N	SD	CV
P4	L= 2.2	2.2	2	-	-
	W= 2.8	2.8	2	-	-
M1	L= 2.3-2.5	2.5	6	0.04	2.5
	W= 3.2	3.2	5	-	-
M2	L= 2.5-2.7	2.6	4	0.07	0.04
	W= 3.8-3.9	3.9	4	0.07	0.04
M3	L= 1.9	1.9	1	-	-
	W= 3.0	3.0	1	-	-
dp4	L= 2.2-2.3	2.3	2	0.1	0.07
	W= 1.2-1.3	1.3	2	0.1	0.07
p4	L= 2.1-2.2	2.1	3	0.05	0.03
	W= 1.3	1.3	3	-	-
m1	L= 2.5-2.7	2.6	8	0.06	0.02
	AW= 1.3-1.7	1.6	8	0.16	0.06
	PW= 1.5-1.8	1.7	8	0.14	0.05
m2	L= 2.5-2.8	2.7	8	0.12	0.43
	AW= 1.7-2.0	1.9	8	0.1	0.04
	PW= 1.8-2.0	1.9	8	0.08	0.03
m3	L= 2.3-2.8	2.6	9	0.11	0.04
	AW= 1.4-1.8	1.6	9	0.09	0.03
	PW= 1.3-1.7	1.4	9	0.08	0.3

Table 25 Measurements and descriptive statistics of the dentition of *Litocherus* sp., cf. *L. notissimus* from the Hand Hills West locality, Upper Level and Lower Level.

P	OR	Mean	N	SD	CV
M1	L= 1.6-1.8	1.7	2	0.1	0.07
	W= 2.5-2.8	2.7	2	0.3	0.2
M3	L= 1.3-1.4	1.4	2	0.05	0.02
	W= 2.1-2.2	2.2	2	0.05	0.02
p3	L= 1.7	1.7	1	-	-
	W= 1.1	1.1	1	-	-
p4	L= 2.1	2.1	1	-	-
	W= 1.4	1.4	1	-	-
m1	L= 1.8-2.1	1.9	7	0.08	0.03
	AW= 1.2-1.5	1.3	7	0.13	0.05
	PW= 1.3-1.4	1.3	7	0.05	0.02
m2	L= 2.0	2.0	1	-	-
	AW= 1.4	1.4	1	-	-
	PW= 1.5	1.5	1	-	-

Table 26 Measurements and descriptive statistics of the dentition of Litocherus sp., cf. L. zygeus from the Hand Hills West locality, Lower Level.

P	OR		Mean	N	SD	CV
M2	L=	2.0-2.3	2.1	5	0.13	0.05
	W=	3.0-3.3	3.2	4	0.1	0.5
p4	L=	3.0	3.0	1	-	-
	W=	1.9	1.9	1	-	-
m1	L=	2.5	2.5	5	-	-
	AW=	1.5-1.8	1.7	5	0.15	0.07
	PW=	1.5-2.0	1.8	5	0.15	0.07
m2	L=	2.1-2.3	2.1	11	0.05	0.02
	AW=	1.5-2.0	1.7	12	0.12	0.04
	PW=	1.6-1.8	1.8	11	0.03	0.01
m3	L=	2.1-2.2	2.1	2	0.1	0.07
	AW=	1.4	1.4	2	-	-
	PW=	1.3-1.4	1.4	2	0.05	0.04

Table 27 Measurements and descriptive statistics of the dentition of Litocherus sp., cf. L. zygeus from the Hand Hills West locality, Upper Level.

P	OR	Mean	N	SD	CV
M3	L= 1.7-2.0	1.8	3	0.15	0.09
	W= 2.6-2.8	2.7	3	0.15	0.09
p4	L= 2.8-3.3	2.8	7	1.12	0.43
	W= 1.4-1.9	1.7	7	0.12	0.05
m1	L= 2.4-2.6	2.5	15	0.06	0.02
	AW= 1.6-1.9	1.8	15	0.05	0.01
	PW= 1.8-2.0	1.9	15	0.08	0.02
m2	L= 2.0-2.2	2.2	11	0.03	0.01
	AW= 1.6-2.0	1.8	11	0.09	0.03
	PW= 1.6-1.9	1.8	11	0.07	0.01
m3	L= 1.9-2.2	2.1	5	0.15	0.07
	AW= 1.3-1.6	1.4	5	0.13	0.06
	PW= 1.6-1.9	1.3	5	0.08	0.04

Table 28 Measurements and descriptive statistics of the dentition of *Leptacodon* sp., cf. *L. packi* from Hand Hills West locality, Upper Level and Lower Level.

P	OR	Mean	N	SD	CV
M1	L= 1.6	1.6	1	-	-
	W= 2.5	2.5	1	-	-
M2	L= 1.3-1.4	1.4	2	0.1	0.07
	W= 1.8	1.8	2	-	-
p3	L= 1.0-1.2	1.1	3	0.02	0.01
	W= 0.6	0.6	3	-	-
p4	L= 1.5-1.6	1.5	10	0.03	0.01
	W= 0.8-1.1	0.9	10	0.11	0.03
m1	L= 1.5-1.8	1.7	8	0.1	0.04
	AW= 1.1-1.2	1.1	8	0.04	0.01
	PW= 0.8-1.2	1.1	8	0.07	0.03
m2	L= 1.4-1.5	1.5	4	0.03	0.02
	AW= 1.1-1.2	1.2	4	0.07	0.04
	PW= 1.1-1.2	1.1	4	0.03	0.02
m3	L= 1.3-1.5	1.4	3	0.15	0.09
	AW= 0.8-0.9	0.9	2	0.1	0.07
	PW= 0.7-0.8	0.8	2	0.1	0.07

Table 29 Measurements and descriptive statistics of the dentition of *Leptacodon* sp., cf. *L. tener* from Hand Hills West locality, Lower Level.

P	OR	Mean	N	SD	CV
M1	L= 1.2	1.2	1	-	-
	W= 1.8	1.8	1	-	-
m1	L= 1.3	1.3	1	-	-
	AW= 1.0	1.0	1	-	-
	PW= 0.8	0.8	1	-	-

Table 30 Measurements and descriptive statistics of the dentition of Nyctitherium sp. from Hand Hills West locality, Upper Level.

P	OR		Mean	N	SD	CV
p1	L=	0.98	0.98	1	-	-
	W=	0.35	0.35	1	-	-
p2	L=	0.98	0.98	1	-	-
	W	0.35	0.35	1	-	-
p3	L=	1.3	1.3	1	-	-
	W=	0.6	0.6	1	-	-
m3	L=	1.2	1.2	1	-	-
	AW=	0.7	0.7	1	-	-
	PW=	0.6	0.6	1	-	-

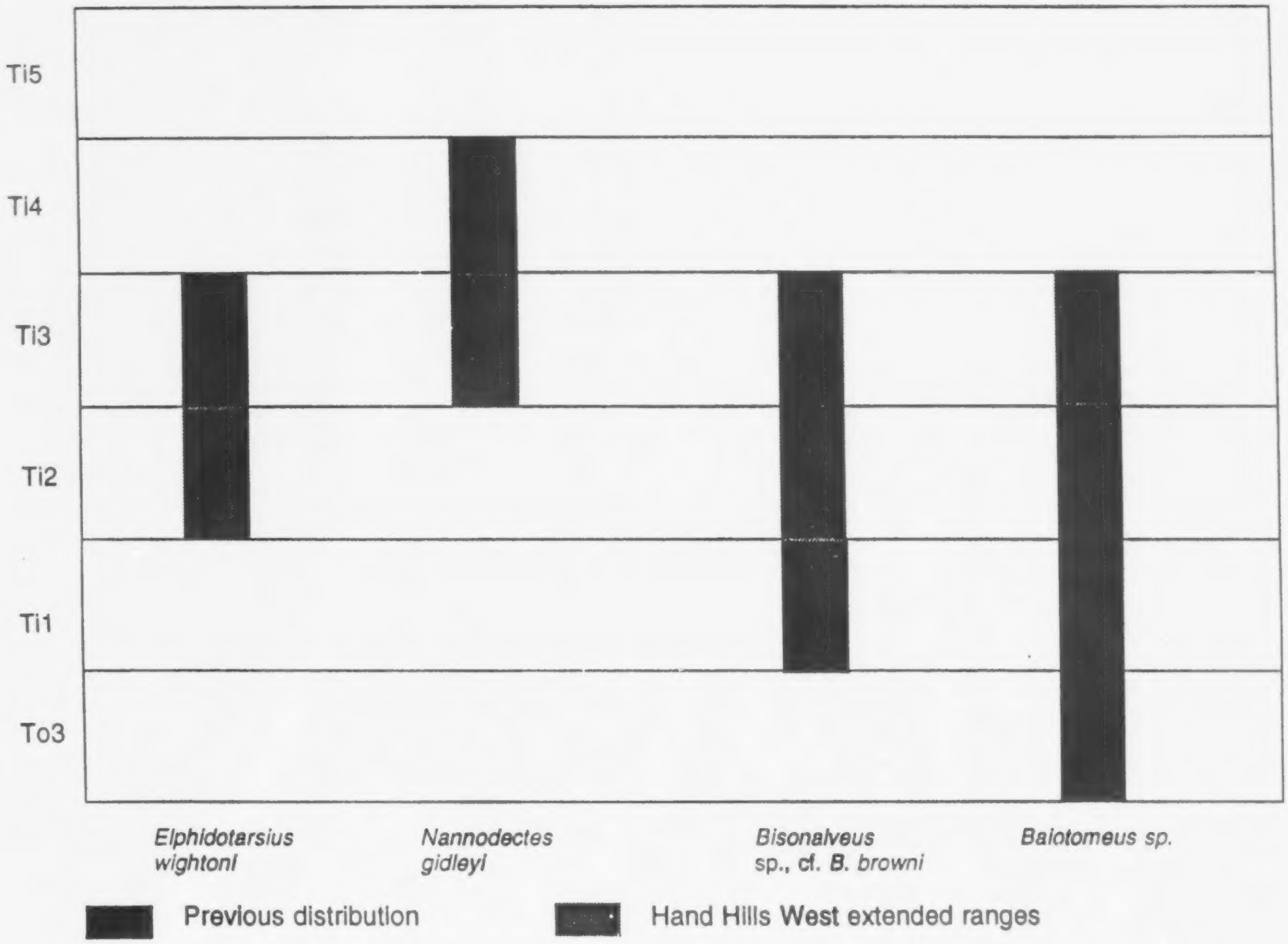

Table 31 Previous distribution and extended geological time ranges for the Hand Hills Fauna.

Table 32 Faunal composition of the Hand Hills West locality, Upper Level and Lower Level.

Species	Upper Level	Lower Level
Order Multituberculata		
Mimetodon silberlingi	X	X
Mesodma pygmaea	X	X
Mesodma sp. P	X	-
Ectypodus sp., cf. *E. szalayi*	X	G
Ectypodus sp.	G	X
Ptilodus sp. C	X	F
Neoplagiaulax hunteri	X	X
Neoplagiaulax sp., cf. *N. hazeni*	X	X
Neoplagiaulax sp.	X	X
Prochetodon foxi	X	-
Baiotomeus sp.	X	-
Order Marsupicarnivora		
Peradectes elegans	X	-
Peradectes sp.	X	-
Order Primates		
Plesiadapis rex	X	-
Nannodectes simpsoni	X	-
Nannodectes gidleyi	X	-
Saxonella naylori	X	-
Carpodaptes hazelae	X	G
Carpodaptes sp., cf. *C. hazelae*	G	X
Elphidotarsius wightoni	X	X
Elphidotarsius russelli	G	X
Zanycteris paleocenus	X	F
Picrodus silberlingi	F	X
Ignacius frugivorus	X	X
cf. Palaechthonidae	X	-
cf. Microsyopidae	X	-
Order Condylartha		
Ectocion cedrus	X	G
Ectocion sp.	G	X
Claenodon sp.	X	-
Dorraletes diminutivus	X	X

Order Uncertain		
Bisonalveus sp., cf. *B. browni*	X	X
Pararyctes pattersoni	X	X
Pararyctes sp. 1	X	X
Pararyctes sp. 2	X	-
Pararyctes sp.	X	-
Propalaeosinopa septentrionalis	X	X
Palaeoryctes sp., cf. *P. punctatus*	X	-
Nyctitherium sp.	X	-
Apatemyidae	X	X
Order Lipotyphla		
Leptacodon sp., cf. *L. packi*	X	X
Leptacodon sp., cf. *L. tener*	G	X
Litocherus sp., cf. *L. zygeus*	X	X
Litocherus sp., cf. *L. notissimus*	X	X
Order Dermoptera		
Elpidophorus elegans	X	X
Order Carnivora		
Protictis	X	-

Table 33 Faunal comparison of Hand Hills West locality, Lower Level and Scarritt Quarry.

Species	[1]HHW	[2]Scarritt Quarry
Order Multituberculata		
Mesodma pygmaea	X	X
Mimetodon silberlingi	X	-
Ptilodus sp.	-	X
Neoplagiaulax sp., cf. *N. hazeni*	X	X
Neoplagiaulax hunteri	X	G
Ectypodus sp.	X	-
Microcosmodon	-	X
Anconodon	-	X
Order Primates		
Plesiadapis anceps	SF	X
Nannodectes simpsoni	SF	X
Carpodaptes sp., cf. *C. hazelae*	X	X
Elphidotarsius wightoni	X	X
Elphidotarsius russelli	X	G
Picrodus silberlingi	X	-
Ignacius frugivorus	X	X
Order Condylartha		
Ectocion sp.	X	-
Thryptacodon cf. *T. australis*	-	X
cf. *Tricentes* sp.	-	X
Diassacus sp.	-	X
Arctocyon	-	X
Dorraletes diminutivus	X	-
Order Uncertain		
Bisonalveus sp., cf. *B. browni*	X	X
Pararyctes pattersoni	X	X
Propalaeosinopa septentrionalis	X	X
Palaeosinopa simpsoni	-	X
Paleotomus senior	-	X
Pararyctes sp.	X	X
Unuchinia	F	X
Order Lipotyphla		
Leptacodon sp., cf. *L. packi*	X	G

Leptacodon sp., cf. *L. tener*	X	X
Litocherus sp., cf. *L. zygeus*	X	G
Litocherus sp., cf. *L. notissimus*	X	X
Order Dermoptera		
Elpidophorus elegans	X	X
Order Pantodonta		
Titanoides zeuxis	-	X
Order Carnivora		
Protictis	-	X

G - Genus present.

SF - Superfamily present.

[1] Hand Hills West locality, Lower Level, Paskapoo Formation, Alberta.

[2] Scarritt Quarry, Melville Formation, eastern Crazy Mountain Basin, Montana (Rose 1981a, Maas and Krause et al. 1995).

Table 34 Faunal comparison of middle Tiffanian (Ti3) localities in western Canada, Cedar Point Quarry (Wyoming), and Brisbane locality (North Dakota).

Species	[1]HHW	[2]Blindman River	Birchwood	[3]Joffre Bridge	[4]Cedar Point	[5]Brisbane
Order Multituberculata						
Mimetodon silberlingi	X	X	X	X	-	-
Mesodma pygmaea	X	X	X	X	-	G
Mesodma sp. P	X	-	-	-	-	G
Baiotomeus sp.	X	-	-	-	-	-
Ectypodus sp., cf. *E. szalayi*	X	G	-	-	-	G
Ectypodus sp., cf. *E. powelli*	G	G	-	-	X	G
Ptilodus sp. C	X	X	X	G	G	G
Ptilodus sp. T	G	X	X	G	G	G
Ptilodus montanus	G	G	G	G	G	X
Prochetodon foxi	G	X	X	G	-	-
Neoplagiaulax hunteri	X	X	X	X	X	X
Neoplagiaulax sp., cf. *N. hazeni*	X	X	X	-	-	-
Microcosmodon woodi	-	X	X	-	-	X
Parectypodus sp.	-	-	-	-	-	X
Order Marsupicarnivora						
Peradectes elegans	X	X	-	X	X	X

Order Primates						
Plesiadapis rex	X	X	X	-	X	X
Nannodectes simpsoni	X	X	-	-	-	G
Nannodectes gidleyi	X	-	-	-	-	G
Saxonella naylori	X	X	F	-	-	-
Carpodaptes hazelae	X	X	X	X	X	G
Carpodaptes sp., cf. *C. cygneus*	G	X	G	G	G	X
Elphidotarsius wightoni	X	X	X	-	-	-
Zanycteris paleocenus	X	X	-	-	-	-
Picrodus sp., cf. *P. silberlingi*	-	-	-	-	X	-
Ignacius frugivorus	X	X	X	X	X	X
cf. Palaechthonidae	X	SF	SF	SF	SF	-
cf. Microsyopidae	X	X	SF	SF	SF	-
Micromomys fremdi	-	X	-	X	-	-
Pronothodectes gaoi	-	-	X	-	-	-
Plesiolestes sp., cf. *P. syroki*	-	-	X	-	-	-
Order Condylartha						
Ectocion cedrus	X	X	X	G	G	G
Ectocion wyomingensis	G	G	G	X	X	X
Claenodon sp., cf. *C. ferox*	G	X	G	-	X	-
Claenodon sp., cf. *C. acrogenius*	G	G	G	G	X	-
Colpoclaenus keeferi	-	X	X	-	-	-
Thyrptacodon australus	-	-	X	-	X	-

Desmatoclaenus mearae	-	-	X	-	-	-
Chriacus sp., cf. *C. pelvidens*	-	-	X	-	G	-
Phenacodus sp.	-	-	X	-	-	-
Metachriacus sp.	-	X	-	-	-	-
Minotricentes sp.	-	-	-	-	X	-
Diassacus sp.	-	-	-	-	X	-
Dorraletes diminutivus	X	-	-	-	-	X
Order Uncertain						
Bisonalveus gracilis	G	X	X	-	-	-
Bisonalveus sp., cf. *B. browni*	X	G	G	-	-	G
Pararyctes pattersoni	X	G	X	X	-	X
Propalaeosinopa septentrionalis	X	X	X	X	X	G
Propalaeosinopa albertensis	G	X	G	X	G	X
Palaeoryctes sp., cf. *P. punctatus*	X	-	-	G	G	X
Nyctitherium sp.	X	-	-	-	-	-
Prodiacodon sp.	-	X	-	-	-	-
Labidolemur soricoides	F	-	F	-	X	-
Unuchinia sp.	F	-	F	-	-	G
Eudaemonema sp., cf. *E. cuspidata*	-	G	X	-	-	-
Myrmecoboides sp.	-	-	-	-	X	-
Mckennatherium sp., cf. *M. ladae*	-	-	-	-	X	-

Order Lipotyphla						
Leptacodon sp., cf. *L. packi*	X	X	X	-	G	-
Leptacodon tener	G	G	G	G	X	X
Leptacodon munusculum	G	G	G	-	X	G
Litocherus sp., cf. *L. zygeus*	X	X	X	X	G	G
Litocherus sp., cf. *L. notissimus*	X	X	-	X	G	G
Litocherus lacunatus	G	G	G	G	G	X
Aphronorus sp.	-	X	-	-	-	-
Diacodocherus minutus	-	X	-	X	-	-
Stilpnodon sp.	-	-	-	X	-	-
Litolestes ignotus	-	-	-	X	G	-
Order Dermoptera						
Elpidophorus elegans	X	X	X	X	X	-
Order Carnivora						
Raphictis sp., cf. *R. gausion*	X	X	-	-		
Protictis paralus	-	X	G	-		
Procticts sp., cf. *P. haydenianus*	-	G	G	-	X	G
Tytthaena parrisi	-	-	-	-	X	-
Miacid sp.	-	-	-	-	-	X
Order Pantodonta						

Titanoides zeuxis	-	-	X	G	X	-
Cyriacotherium sp., cf. *C. argyreum*	-	X	X	-	X	-

G - Genus present.
SF - Superfamily present.
F - Family present.

[1] Hand Hills West locality, Upper Level, Paskapoo Formation.

[2] UADW-1, UADW-2, UADW-3 localities, Paskapoo Formation, Blindman River (Fox 1990).

[3] Joffre Bridge Roadcut Lower Level, Upper Level, and Joffre Bridge Mammal Site No. 1, Paskapoo Formation, Red Deer River (Fox 1990).

[4] Cedar Point Quarry, Polecat Bench Formation, Wyoming (Rose 1981a).

[5] Brisbane locality, Tongue River Formation, North Dakota (Holtzman 1978).

Table 35 Faunal comparison of generic composition of Tiffanian localities in western Canada.

Genus	^{1}Ti1	^{2}Ti2	^{3}Ti3	^{4}Ti4
Order Multituberculata				
Mimetodon	X	X	X	X
Mesodma	X	X	X	X
Ectypodus	X	X	X	X
Ptilodus	X	-	X	X
Prochetodon	-	-	X	X
Neoplagiaulax	X	X	X	X
Microcosmodon	-	-	X	X
Parectypodus	X	-	-	-
Anconodon	X	-	-	-
Archeronodon	X	-	-	-
Pentacosmodon	X	-	-	-
Baiotomeus	X	-	X	-
Order Marsupicarnivora				
Peradectes	X	-	X	X
Order Primates				
Plesiadapis	X	-	X	X
Nannodectes	X	-	X	X
Saxonella	-	-	X	-
Carpodaptes	X	X	X	X
Elphidotarsius	X	X	X	-
Zanycteris	-	-	X	-
Picrodus	X	X	-	-

Ignacius	X	X	X	X
Micromomys	-	-	X	X
Pronothodectes	X	-	X	-
Plesiolestes	X	-	X	-
Palaecthon	X	-	-	-
Order Condylartha				
Ectocion	X	X	X	X
Claenodon	X	-	X	X
Colpoclaenus	X	-	X	X
Thyrptacodon	X	-	X	X
Desmatoclaenus	X	-	X	-
Chriacus	X	-	X	X
Phenacodus	-	-	X	-
Metachriacus	-	-	X	-
Mimotricentes	X	-	X	-
Dorraletes	-	X	X	-
Oxyprimus	X	-	-	-
Litomylus	X	-	-	-
Order Uncertain				
Bisonalveus	X	X	X	-
Pararyctes	X	X	X	X
Propalaeosinopa	X	X	X	X
Palaeoryctes	X	-	X	-
Prodiacodon	X	-	X	-
Labidolemur	-	X	X	-
Eudaemonema	X	-	X	-
Myrmecoboides	X	-	-	-

Paleotomus	X	-	-	-
Jepsenella	X	-	-	-
Order Lipotyphla				
Leptacodon	X	X	X	X
Litocherus	X	X	X	X
Nyctitherium	X	-	X	X
Aphronorus	-	-	X	-
Diacodocherus	-	-	X	X
Stilpnodon	-	-	X	-
Litolestes	-	-	X	X
Limaconyssus	X	-	-	-
Order Dermoptera				
Elpidophorus	X	X	X	X
Order Carnivora				
Raphictis	-	-	X	X
Protictis	-	-	X	X
Pristinictis	X	-	-	-
Simpsonictis	X	-	-	-

Order Pantodonta				
Titanoides	-	-	X	X
Cyriacotherium	-	-	X	X

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[1] Cochrane 2 locality, Porcupine Hills Formation (Youzwyshyn 1988).

[2] Hand Hills West locality, Lower Level, Paskapoo Formation.

[3] UADW-1, UADW-2, UADW-3 localities, Paskapoo Formation, Blindman River (Fox 1990), Joffre Bridge Roadcut lower level, upper level, and Joffre Bridge Mammal Site No. 1, Paskapoo Formation, Red Deer River (Fox 1990), Birchwood locality, Paskapoo Formation (M.W. Webb in prep.).

[4] Police Point locality, Ravenscrag Formation (Fox 1990), Canyon Ski locality, Paskapoo Formation, Alberta (Fox 1990), Crestomere School locality (Fox 1990), Swan Hills locality, Paskapoo Formation (Fox 1990, Stonely 1988), Roche Perceé, Ravenscrag Formation, Saskatchewan (Krause 1977, 1978, Fox 1990).

Table 36 Species richness and eveness indices for selected Tiffanian localities (modified from Rose 1981b).

	Cedar Point	Scarrit	Brisbane	Princeton	[1]Upper Level	[2]Lower Level
Simpson's index	0.877	0.811	0.973	0.937	0.936	0.893
Shannon-Weiner	2.64	2.03	3.22	2.97	2.94	2.68
Whittaker's index	18.1	11.2	42.3	24.6	23.5	40.9
Pielou index	0.73	0.73	0.95	0.83	0.81	0.81

[1] Hand Hills West Upper Level.
[2] Hand Hills West Lower Level.

Table 37 Completeness (CI and CI_{bda}) and standing generic richness (N_{sr}) indices of Tiffanian localities in western Canada. Generic richness taken from Fox (1990).

	CI	CI_{bda}	N_{sr}	Genera	Species
Ti1	-	-	-	[1]65	86
Ti2	50	44	32.5	18	40
Ti3	100	100	28	47	64
Ti4	-	-	-	30	37

[1] The generic and species richness for the earliest Tiffanian Cochrane 2 locality includes indeterminate genera and species, not included on Table 34 (Youzwyshyn 1988).

CI is the completness index based on the total number of genera known from an interval.
CI_{bda} is a more conservative completeness index based on the number of genera actually known from an interval (see Appendix).

Table 38 Completeness (CI and CI_{bda}) and standing generic richness (N_{sr}) indices of Tiffanian localities in the Bighorn Basin (Montana), and Crazy Mountain Basin (Wyoming) (Mass et al. 1995). Species richness taken from Maas et al. (1995), Krause and Maas (1990), and Rose (1981). Generic richness for North America indicated in parentheses (Krause and Maas 1990).

	CI	CI_{bda}	N_{sr}	Genera	Species
Ti1	90	78	31.0	40 (53)	48
Ti2	68	58	32.5	36 (37)	36
Ti3	95	90	34.0	43 (63)	38
Ti4	55	35	33.0	38 (44)	36

CI is the completness index based on the total number of genera known from an interval.
CI_{bda} is a more conservative completeness index based on the number of genera actually known from an interval (see Appendix).

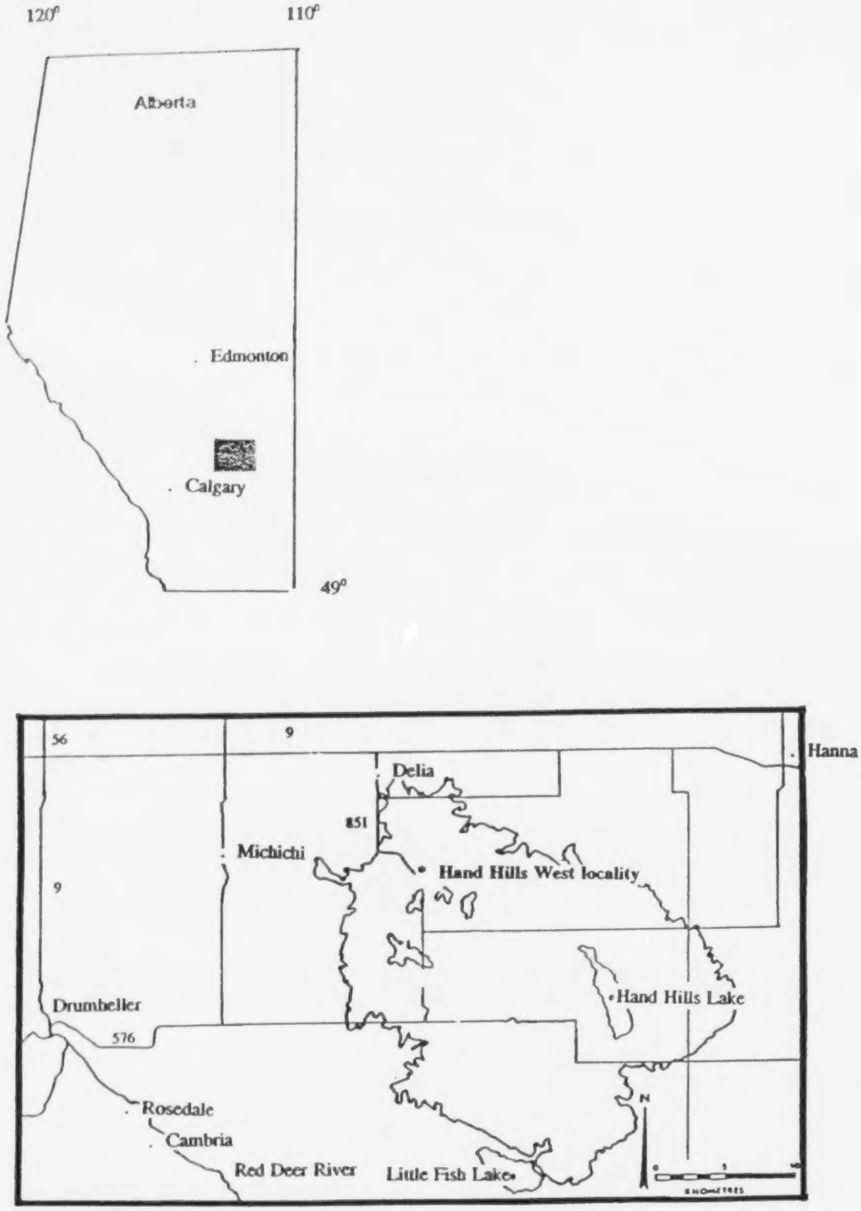
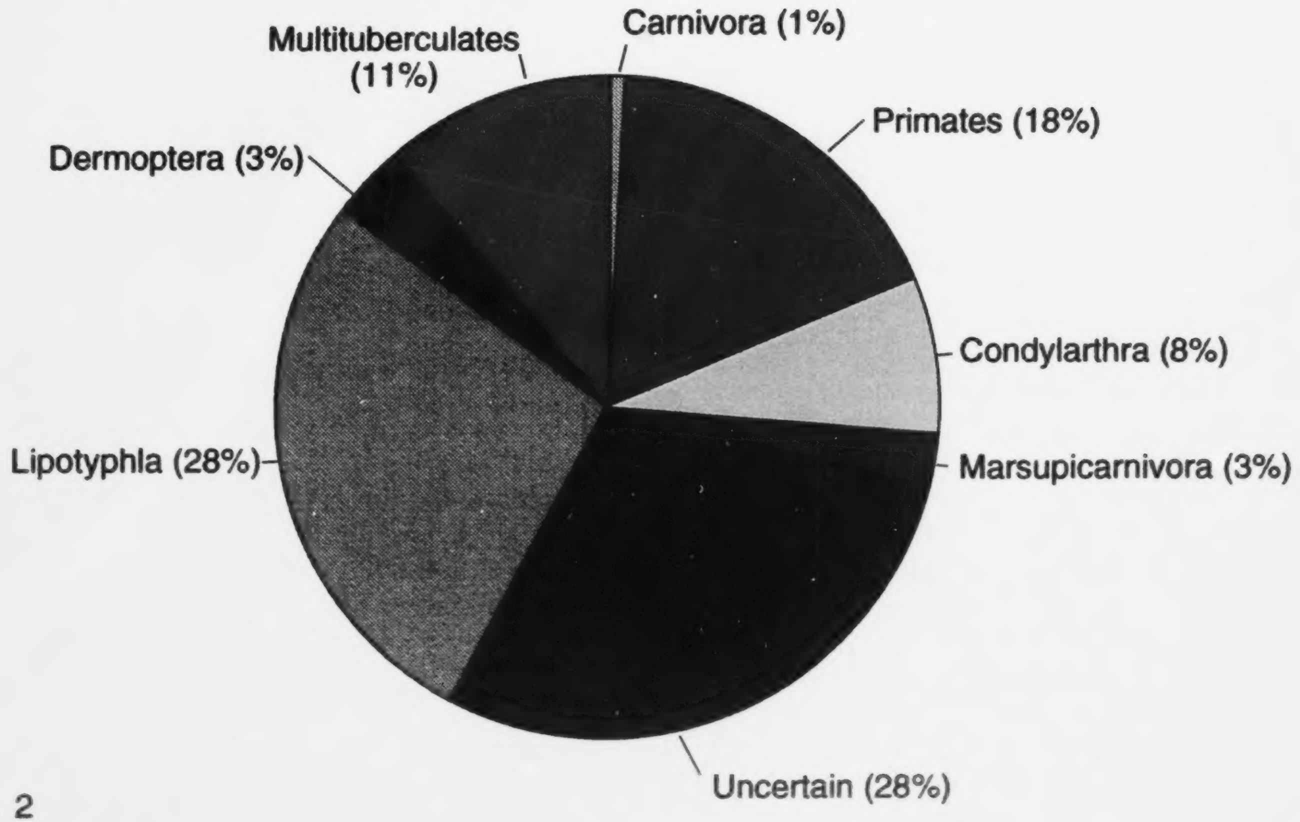

120°
110°
Alberta
Edmonton
Calgary
49°
56
9
Delia
Hanna
851
Michichi
Hand Hills West locality
9
Hand Hills Lake
Drumheller
576
Rosedale
Cambria
Red Deer River
Little Fish Lake
N
KILOMETRES

Figure 1 Map of Alberta and the Hand Hills in southeastern Alberta, with the location of the Hand Hills West locality.



Faunal Composition of Upper Level
Relative Abundance of Mammalian Orders

Figure 2

Faunal Composition of Lower Level
Relative Abundance of Mammalian Orders

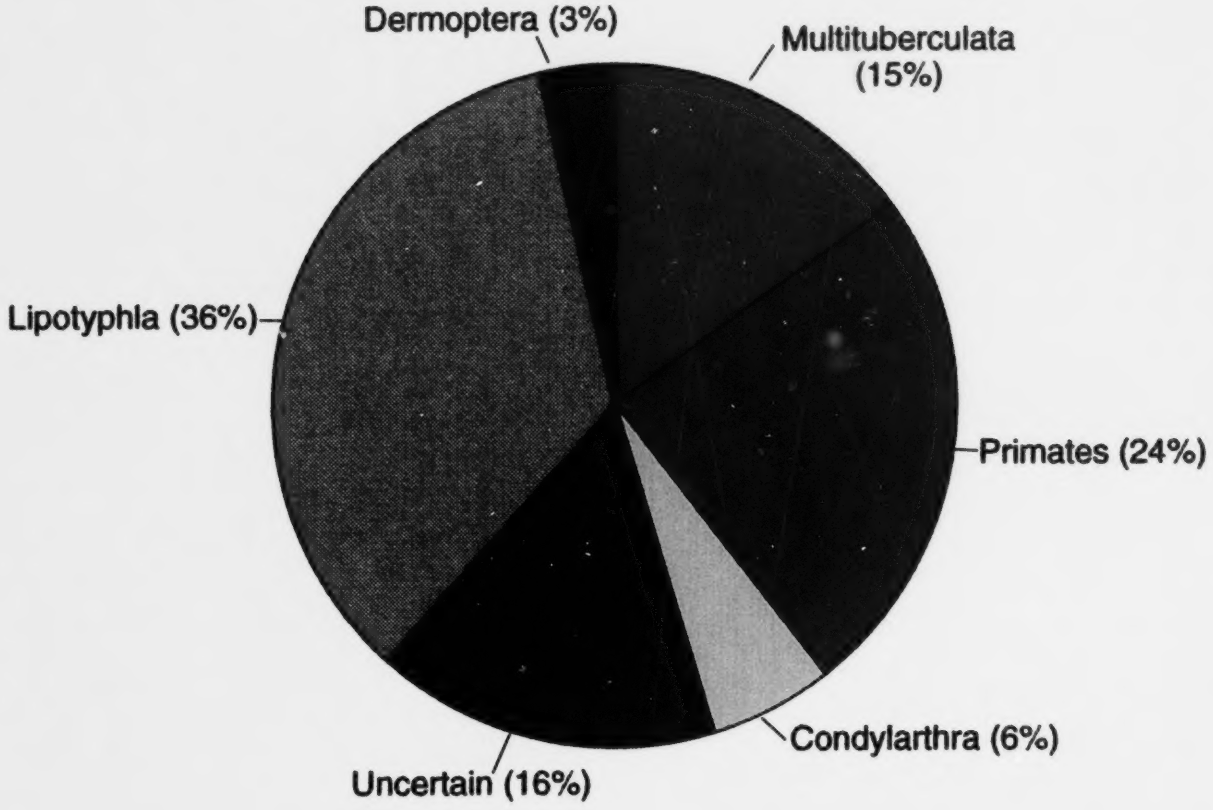


Figure 3

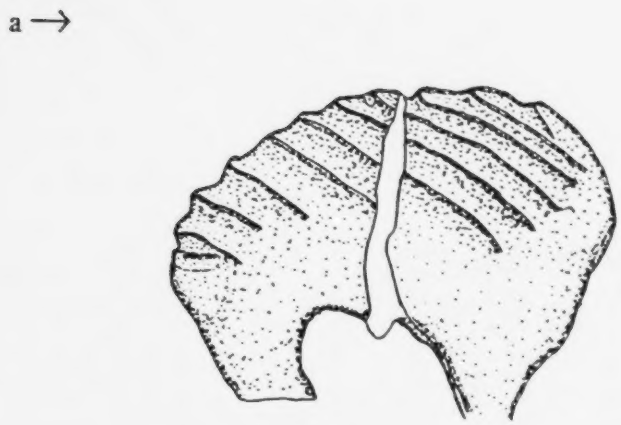


Figure 4a UALVP 34949, rp4, labial view, x31, *Mimetodon silberlingi*.

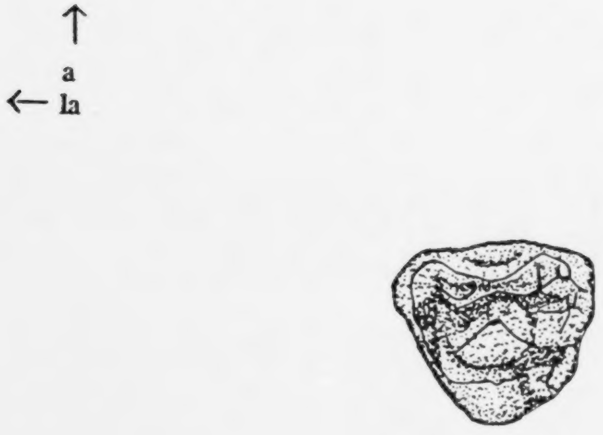


Figure 4b UALVP 35227, RM2, occlusal view, x31, *Mimetodon silberlingi*.

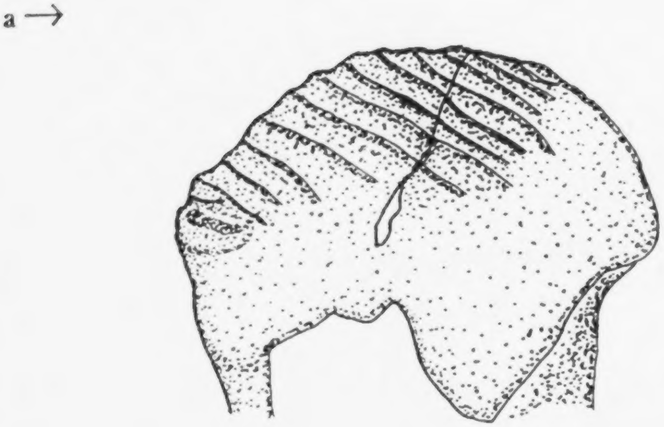


Figure 5a UALVP 34949, rp4, labial view, x31, Mesodma pygmaea.

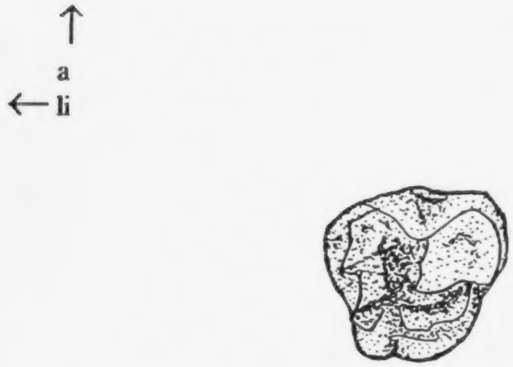


Figure 5b UALVP 35223, LM2, occlusal view, x31, Mesodma pygmaea.

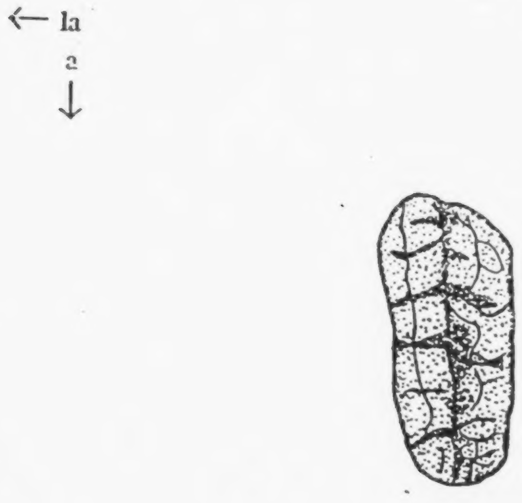


Figure 5c UALVP 34951, rm1, occlusal view, x31, Mesodma pygmaea.

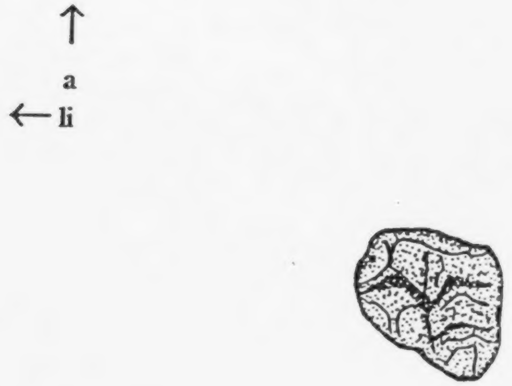


Figure 5d UALVP 34953, rm2, occlusal view, x31, Mesodma pygmaea.

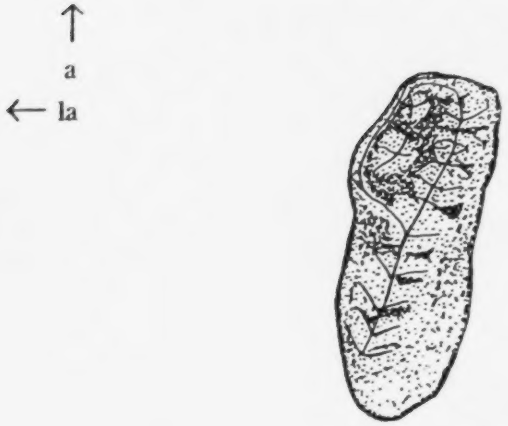


Figure 6 UALVP 34964, RP4, occlusal view, x31, Mesodma sp. P..

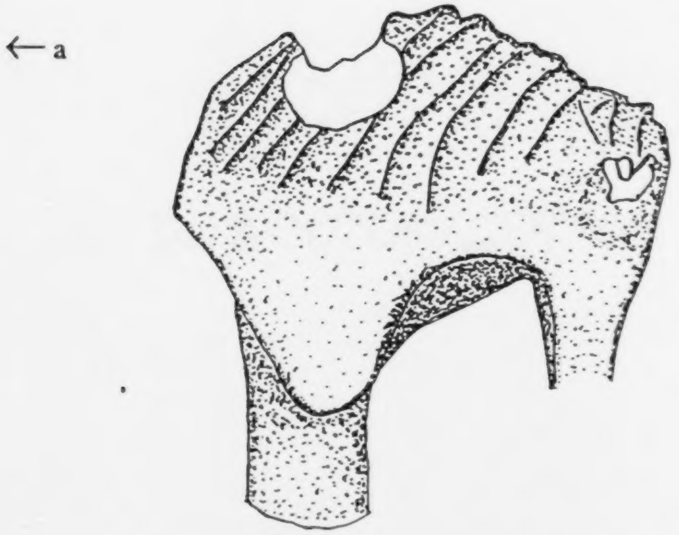


Figure 7 UALVP 34950, lp4, labial view, x22, Mesodma sp..

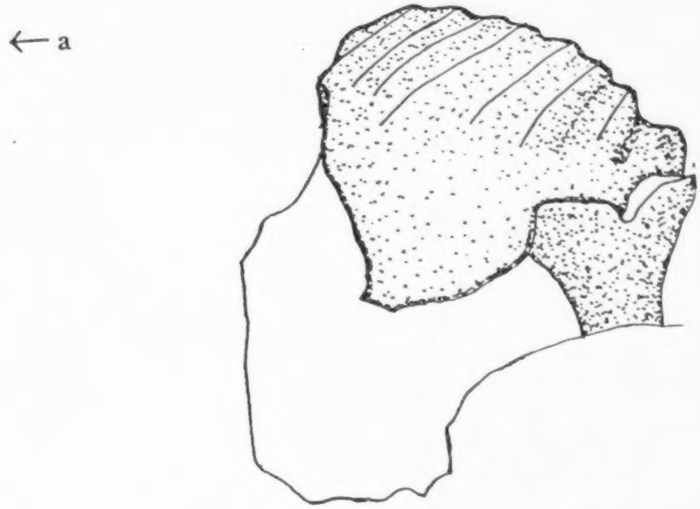


Figure 8a UALVP 34959, lp4, labial view, x31, *Ectypodus* sp., cf. *E. szalayi*.

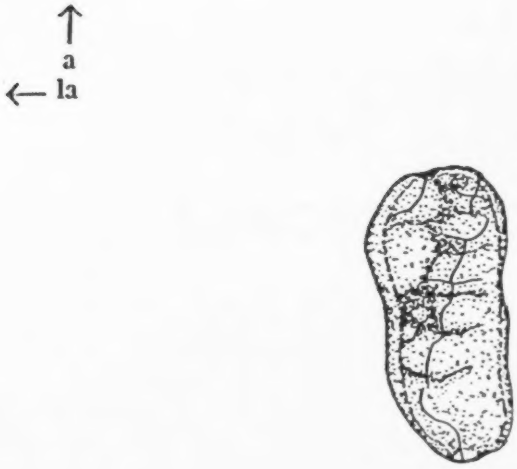


Figure 8b UALVP 34961, RP4, occlusal view, x31, *Ectypodus* sp., cf. *E. szalayi*.

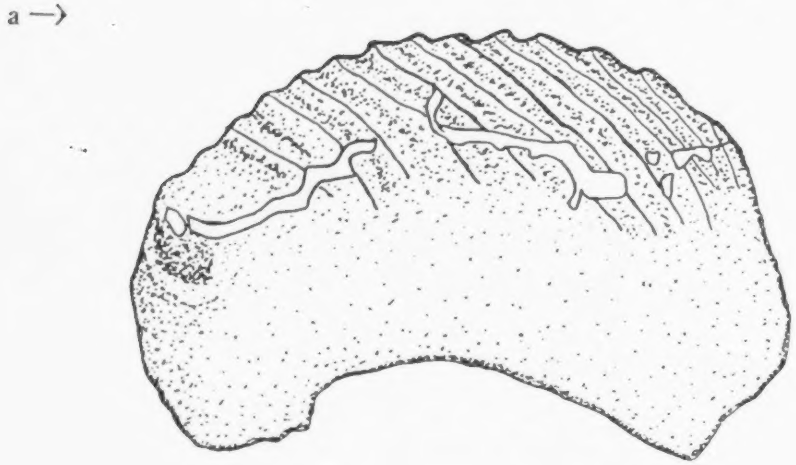


Figure 9a UALVP 34988, rp4, labial view, x25, *Neoplagiaulax* sp., cf. *N. hazeni*.

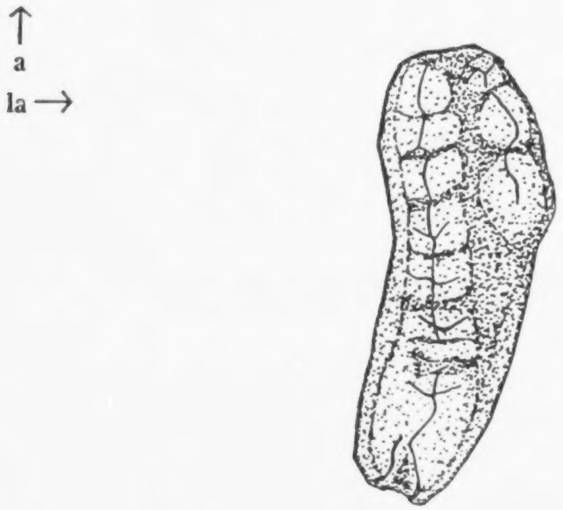


Figure 9b UALVP 34994, LP4, occlusal view, x25, *Neoplagiaulax* sp., cf. *N. hazeni*.

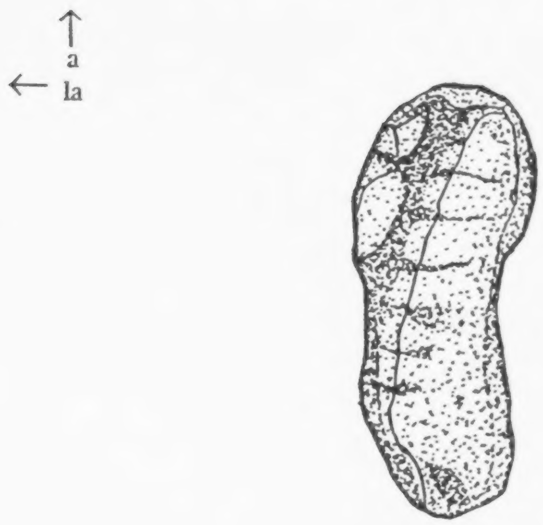


Figure 10a UALVP 34992, RP4, occlusal view, x25, Neoplagiaulax hunteri.

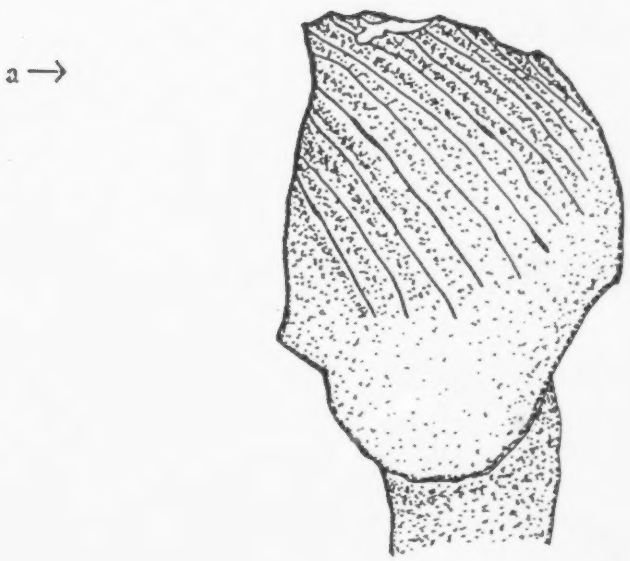


Figure 10b UALVP 34985, lp4, labial view, x25, Neoplagiaulax hunteri.

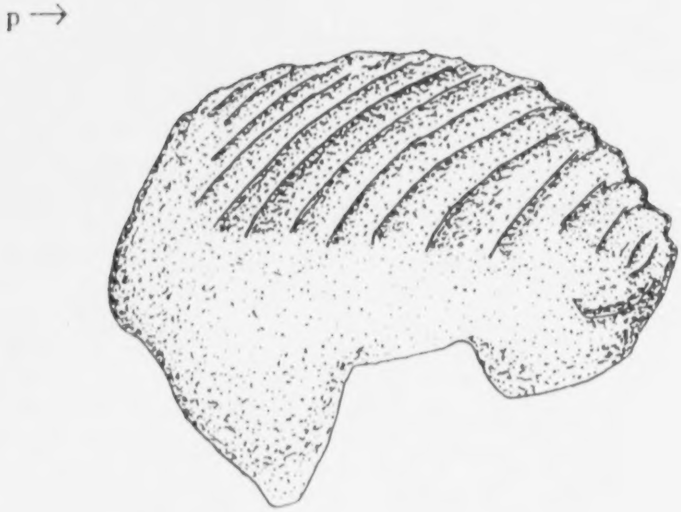


Figure 11a UALVP 34946, lp4, labial view, x25, Neoplagiaulax sp..

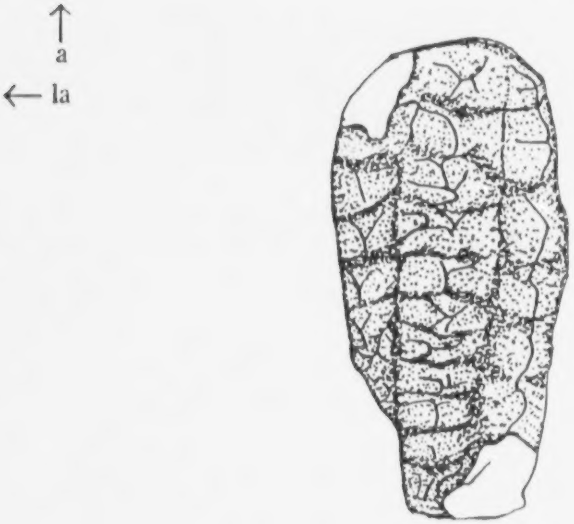


Figure 11b UALVP 35238, RM1, occlusal view, x31, Neoplagiaulax sp..

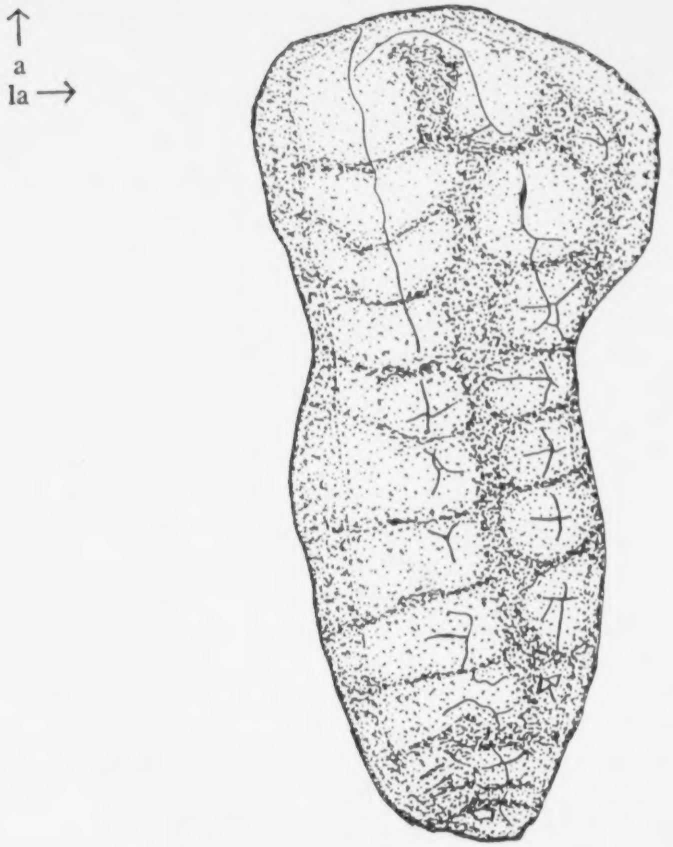


Figure 12a UALVP 34972, LP4, occlusal view, x25, Ptilodus sp. C..

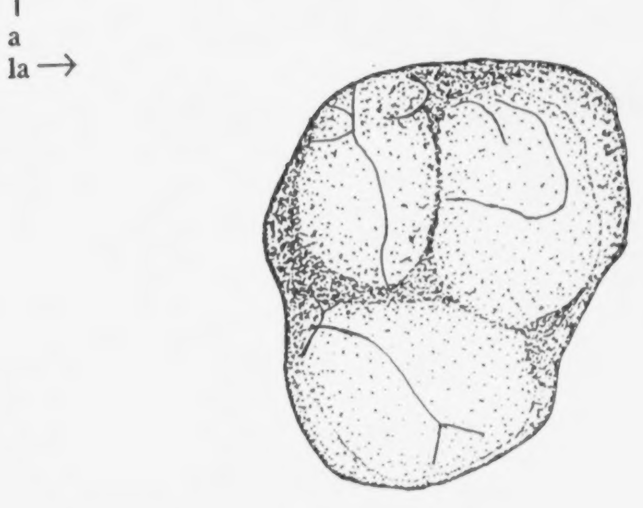


Figure 12b UALVP 34976, LP1, occlusal view, x25, Ptilodus sp. C..

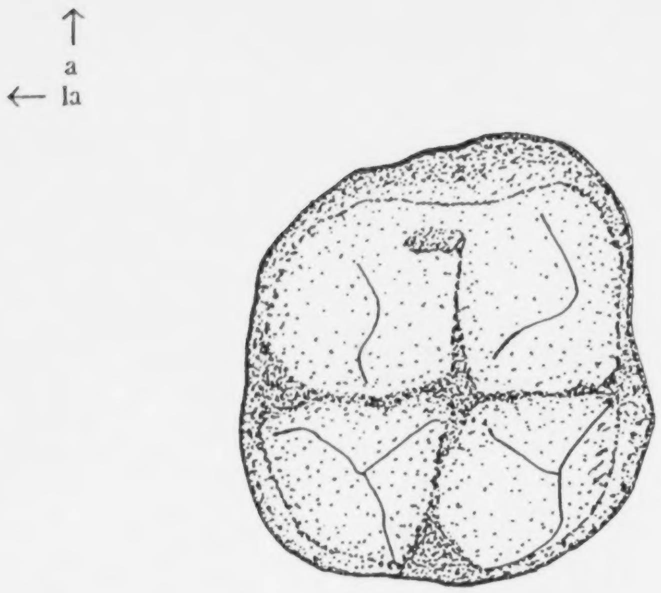


Figure 12c UALVP 34979, LP2, occlusal view, x25, Ptilodus sp. C..

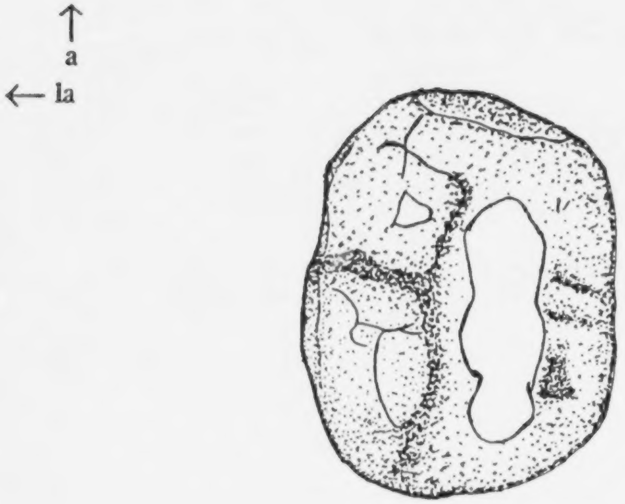


Figure 12d UALVP 34980, LP3, occlusal view, x25, Ptilodus sp. C..

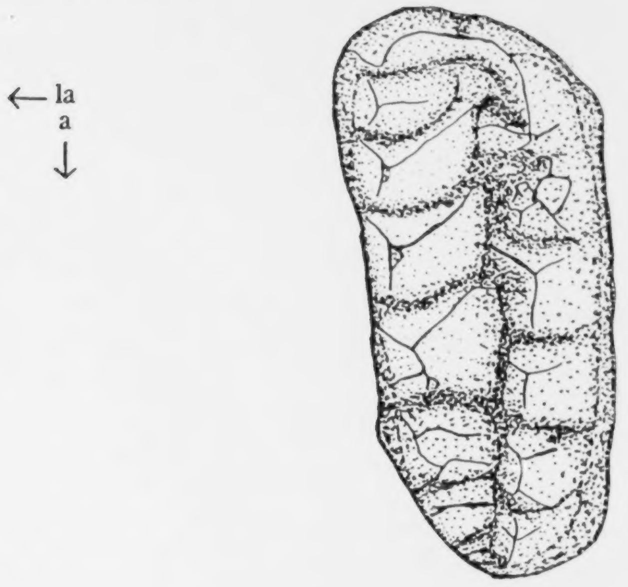


Figure 12e UALVP 34974, rm1, occlusal view, x25, Ptilodus sp. C..

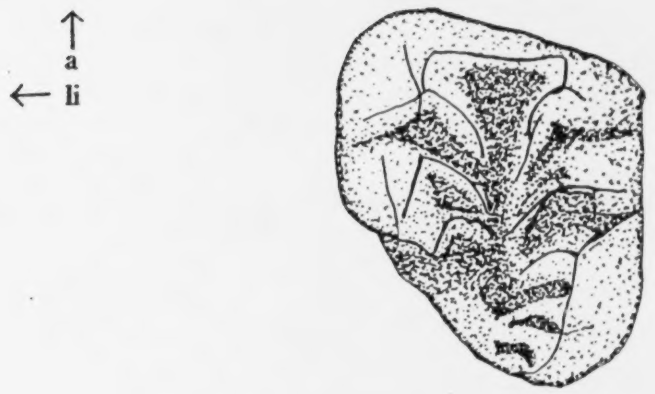


Figure 12f UALVP 34975, rm2, occlusal view, x25, Ptilodus sp. C..

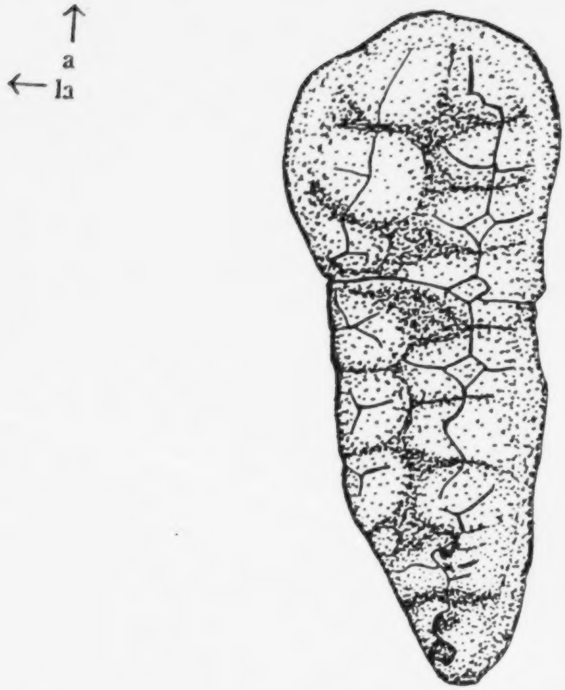


Figure 12g UALVP 34981, RP4, occlusal view, x25, Ptilodus sp..

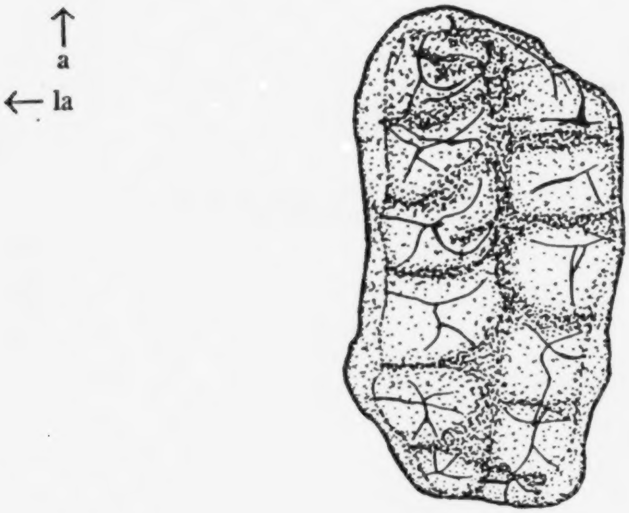


Figure 12h UALVP 34983, rm1, occlusal view, x25, Ptilodus sp..

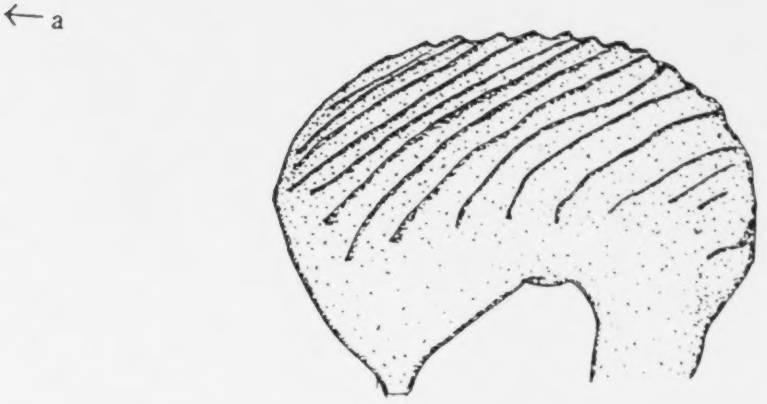


Figure 13 UALVP 34987, lp4, labial view, x10, Prochetodon sp., cf. P. foxi.

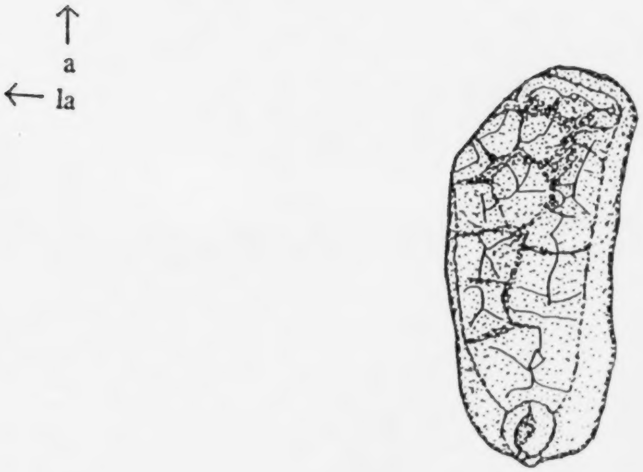


Figure 14 UALVP 34954, RP4, occlusal view, x31, Baiotomeus sp..

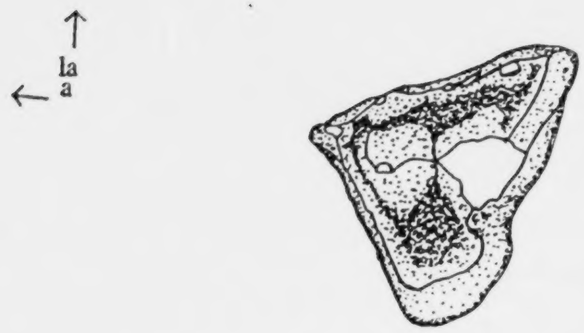


Figure 15a UALVP 34903, LM1, occlusal view, x31, *Peradectes elegans*.

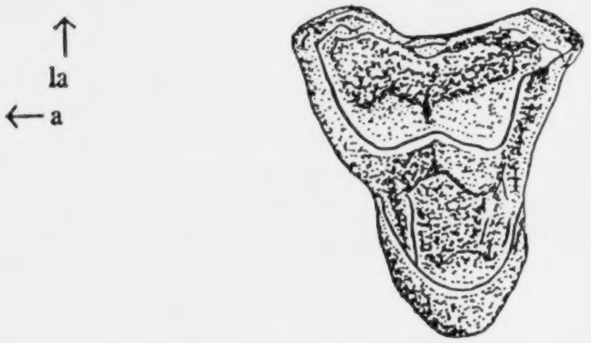


Figure 15b UALVP 34905, RM3, occlusal view, x31, *Peradectes elegans*.

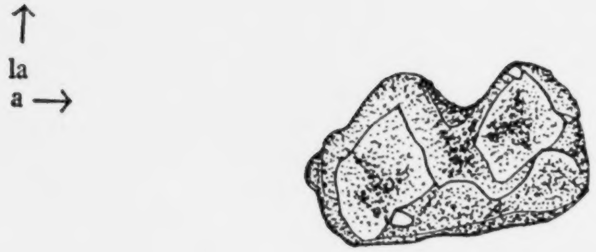


Figure 15c UALVP 34925, rm2, occlusal view, x31, *Peradectes elegans*.

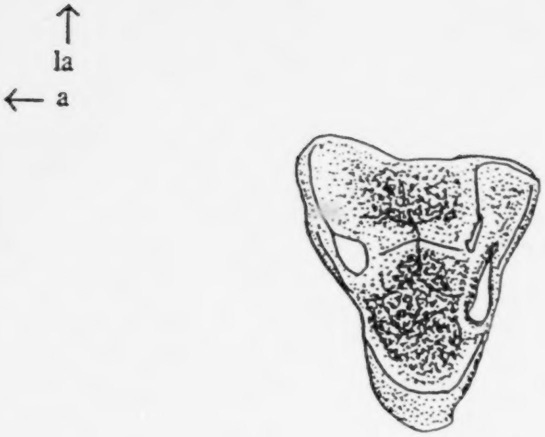


Figure 16a UALVP 34906, RM3, occlusal view, x31, Peradectes sp..

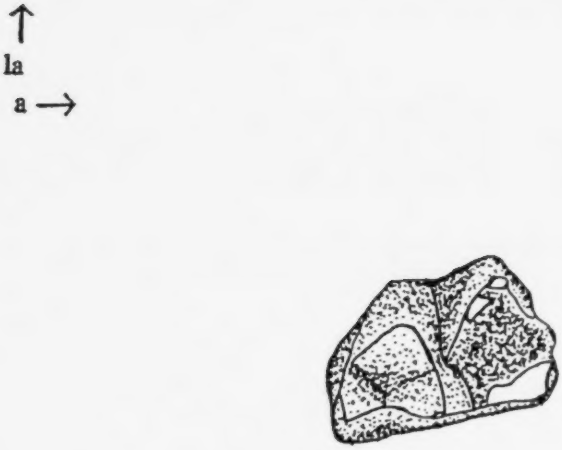


Figure 16b UALVP 34926, rm2, occlusal view, x31, Peradectes sp..

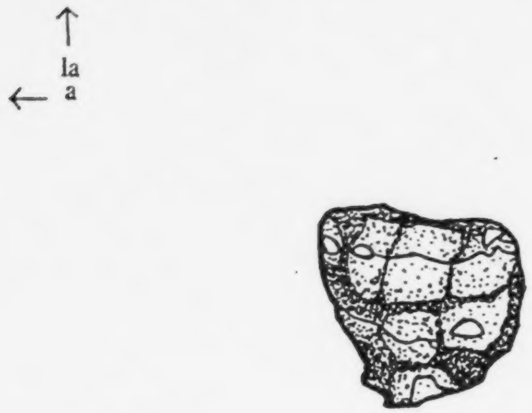


Figure 17a UALVP 34862, LP4, occlusal view, x25, *Elphidotarsius wightoni*.

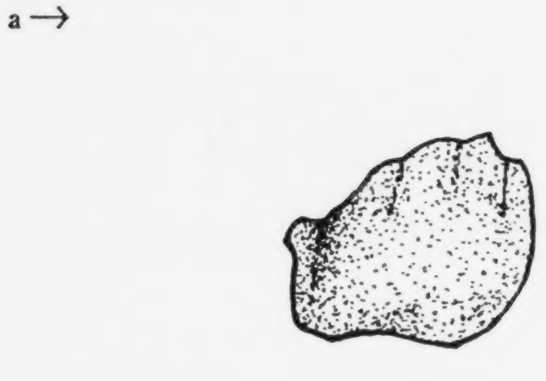


Figure 17b UALVP 34865, rp4, labial view, x25, *Elphidotarsius wightoni*.

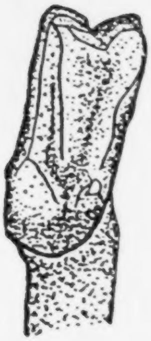


Figure 18a UALVP 34868, RI1, occlusal view, x25, *Elphidotarsius russelli*.

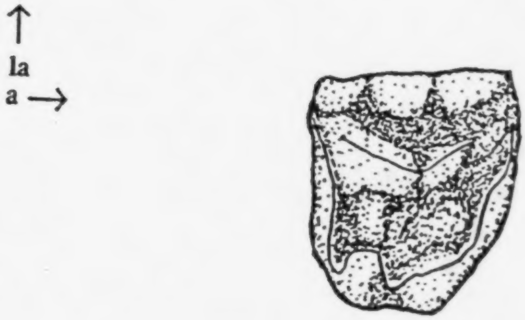


Figure 18b UALVP 34861, LP3, occlusal view, x25, *Ephidotarsius russelli*.

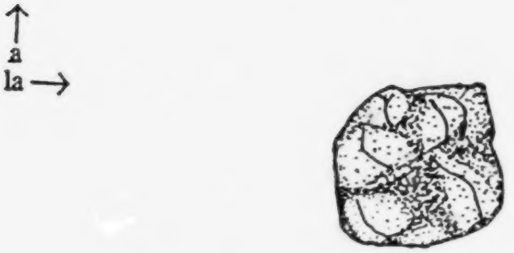


Figure 18c UALVP 34867, rm1, occlusal view, x25, *Elphidotarsius russelli*.

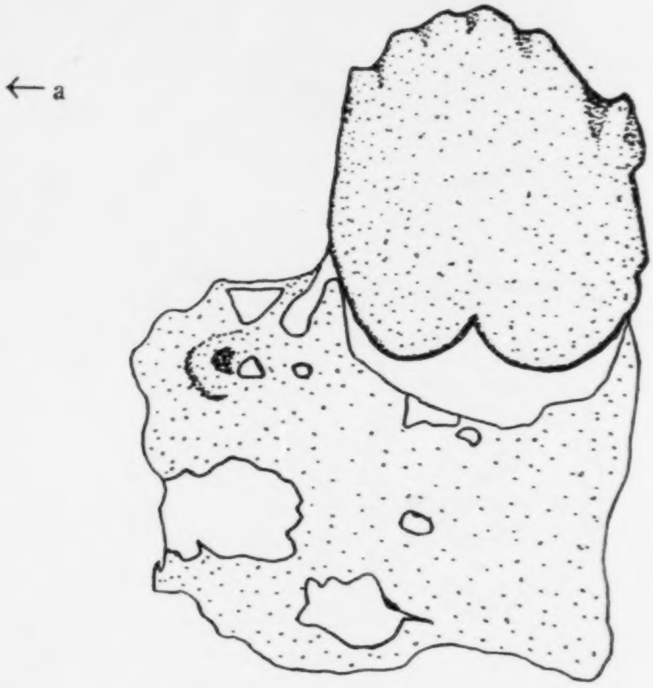


Figure 19 UALVP 34948, rp4, labial view, x25, *Carpodaptes hazelae*.

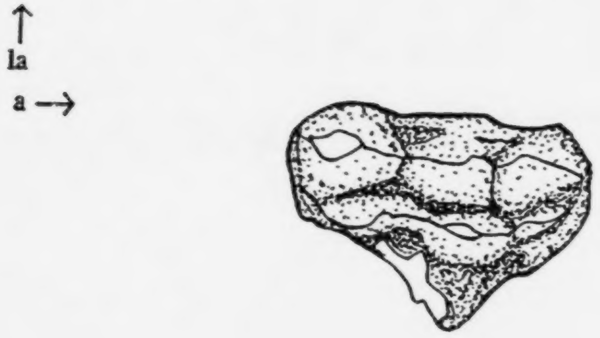


Figure 20 UALVP 34869 LDP4, occlusal view, x25, ?*Carpodaptes hazelae*.

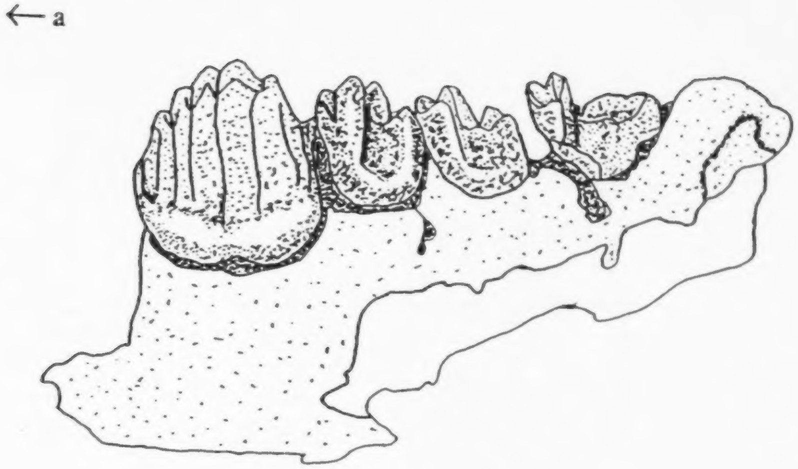


Figure 21a UALVP 34860 lp4-m3, labial view, x12, Carpodaptes sp., cf. C. hazelae

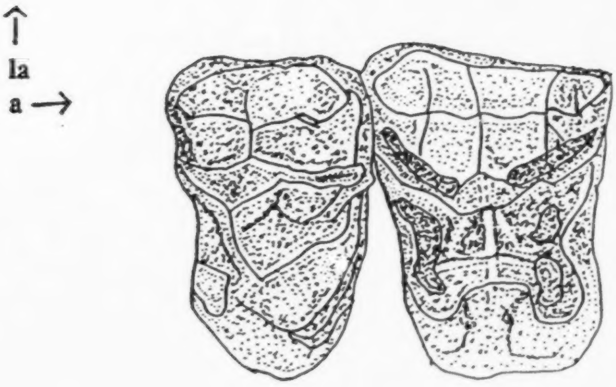


Figure 21b UALVP 34858 RP4-M1, occlusal view, x25, Carpodaptes sp., cf. C. hazelae

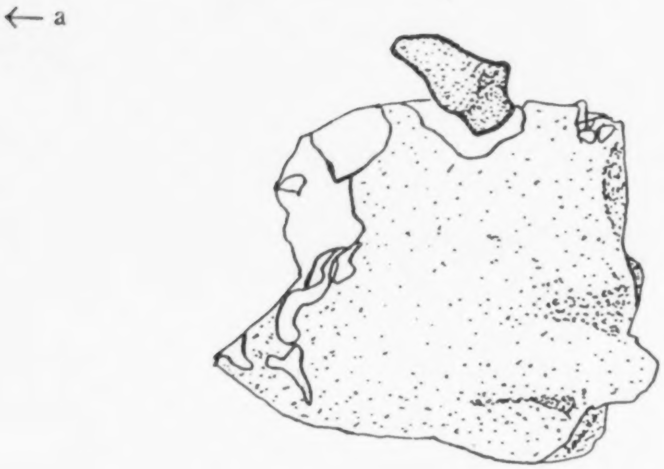


Figure 21c UALVP 35272 lc, labial view, x25, Carpodaptes sp., cf. C. hazelae.

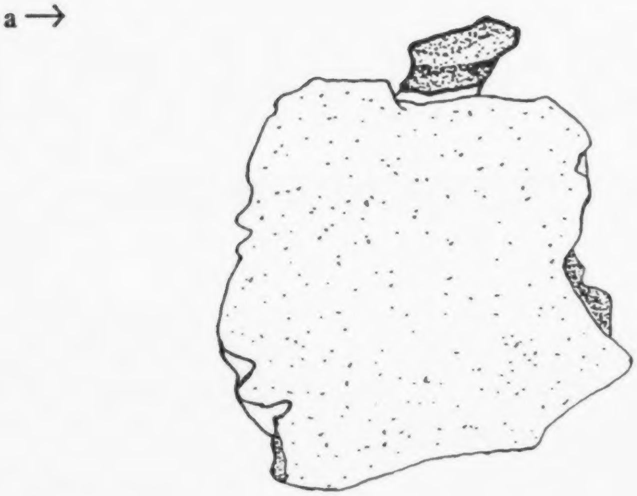


Figure 21d UALVP 35272, lc, lingual view, x25, Carpodaptes sp., cf. C. hazelae.

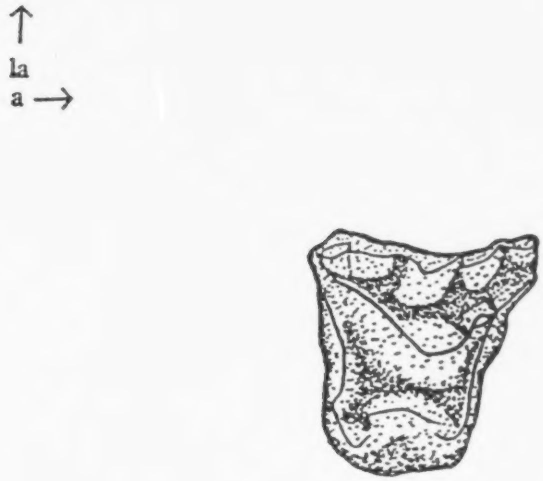


Figure 21e UALVP 34856, RP4, occlusal view, x25, *Carpodaptes* sp., cf. *C. hazelae*.

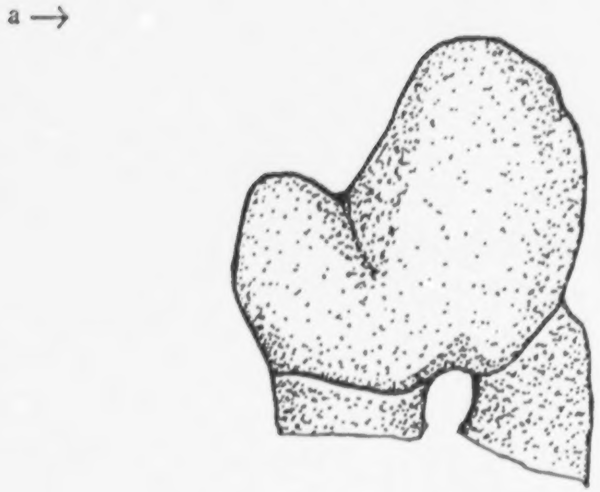


Figure 22a UALVP 34875, rp4, labial view, x25, Plesiadapis rex.

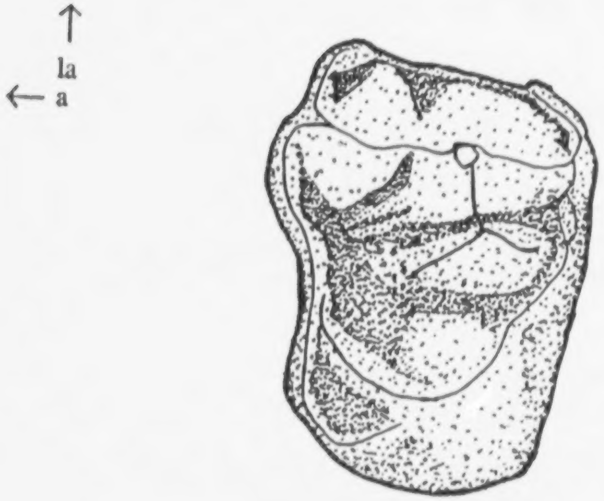


Figure 22b UALVP 34887, LP4, occlusal view, x25, Plesiadapis rex.

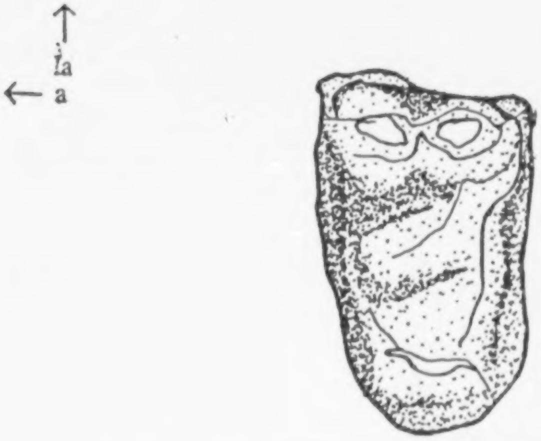


Figure 23 UALVP 34888, LP3, occlusal view, x25, *Plesiadapis* sp., cf. *P*. *rex*.

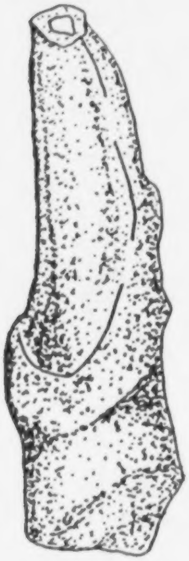


Figure 24a UALVP 34883, LI1, occlusal view, x11, Nannodectes simpsoni.

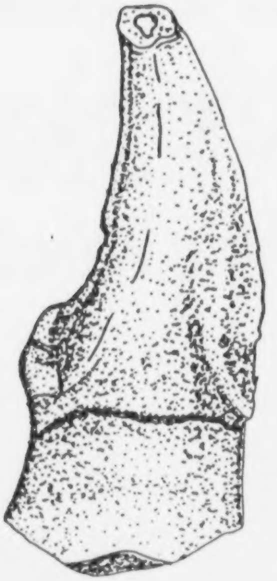


Figure 24b UALVP 34883, LI1, lateral view, x11, Nannodectes simpsoni.

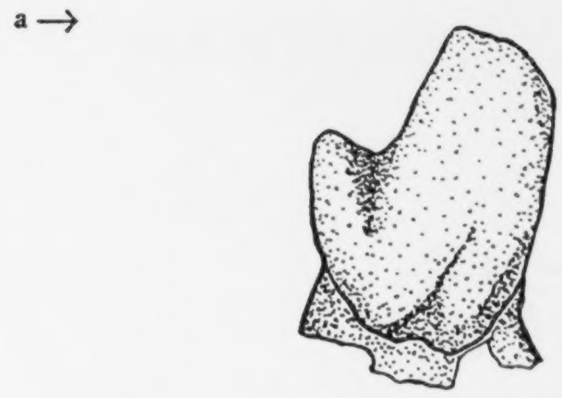


Figure 24c UALVP 34879, rp3, labial view, x25, Nannodectes simpsoni.

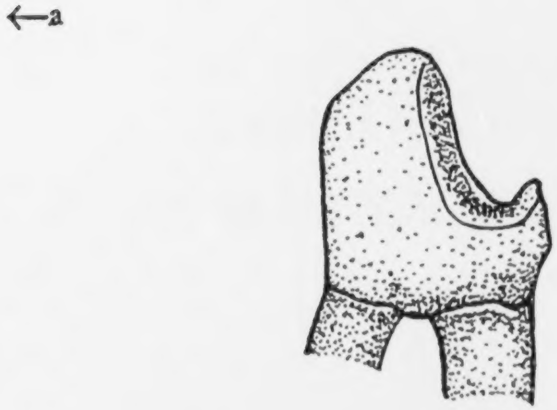


Figure 24d UALVP 34879, rp3, lingual view, x25, Nannodectes simpsoni.

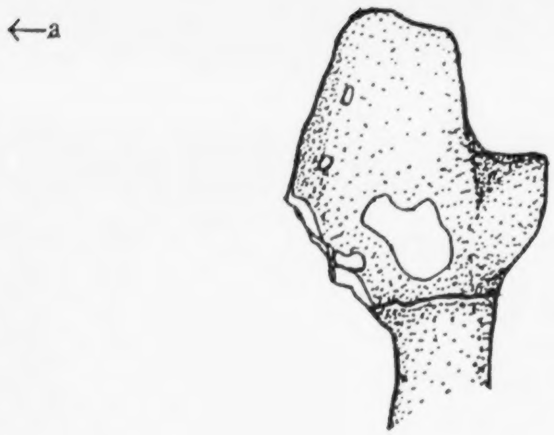


Figure 24e UALVP 34877, lp4, labial view, x25, Nannodectes simpsoni.

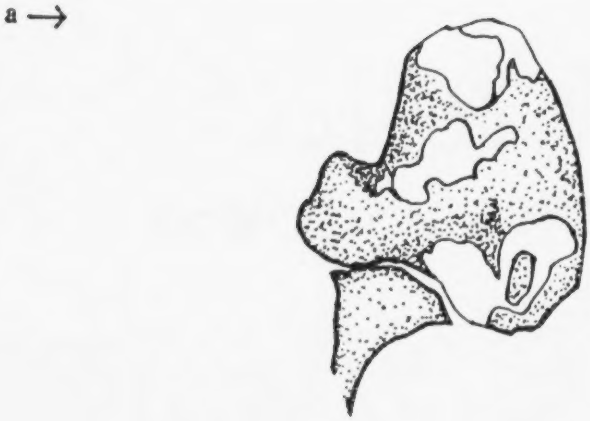


Figure 24f UALVP 34877, lp4, lingual view, x25, Nannodectes simpsoni.

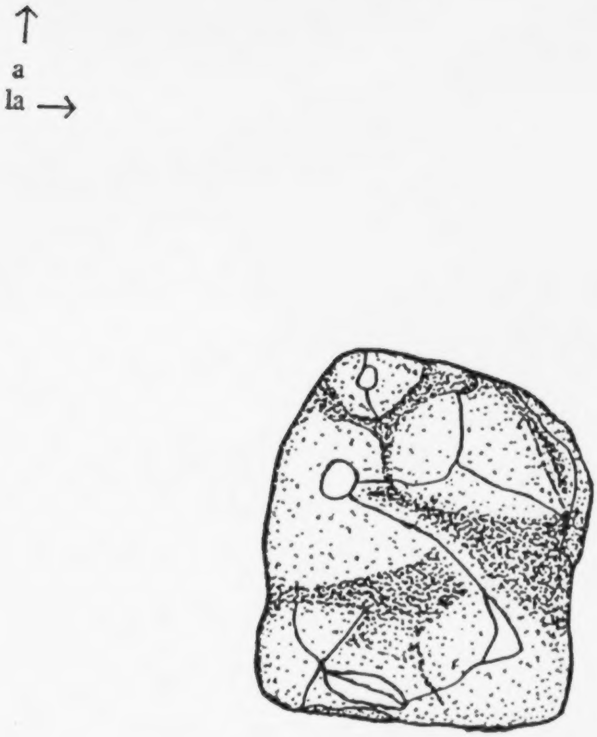


Figure 25 UALVP 34882, rm1, occlusal view, x25, *Nannodectes gidleyi*.

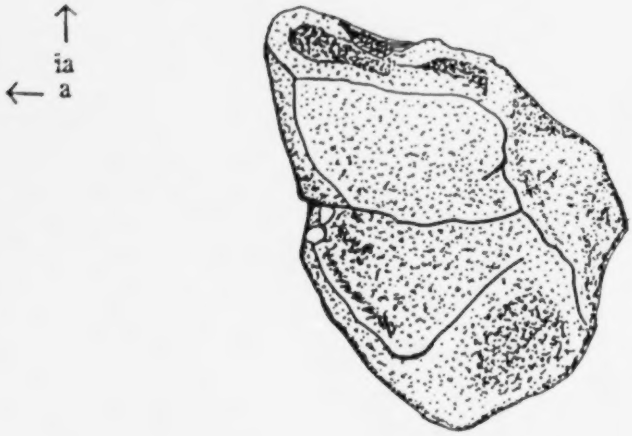


Figure 26 UALVP 34845, RM1, occlusal view, x31, Zanycteris paleocenus.

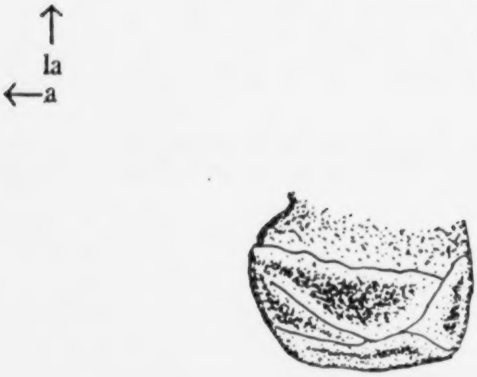


Figure 27 UALVP 34846, LM2, occlusal view, x31, Picrodus silberlingi.

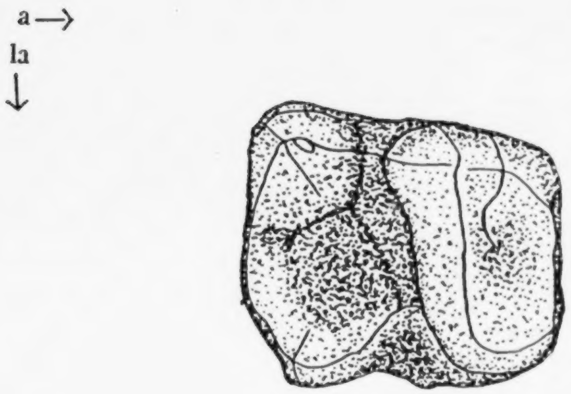


Figure 28a UALVP 34894, rm2, occlusal view, x31, *Ignacius frugivorus*.

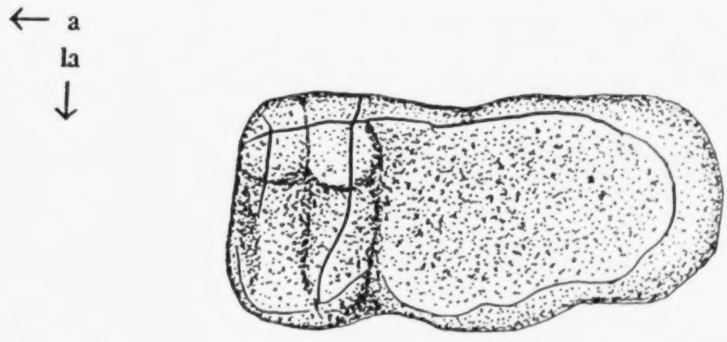


Figure 28b UALVP 34891, lm3, occlusal view, x31, *Ignacius frugivorus*.

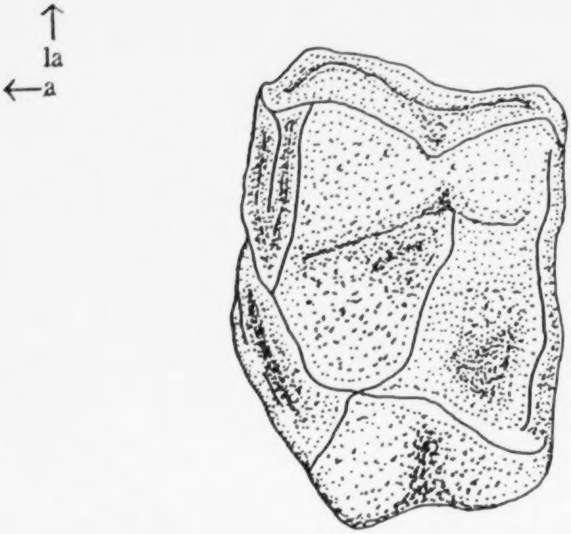


Figure 28c UALVP 34892, LM1, occlusal view, x31, *Ignacius frugivorus*.

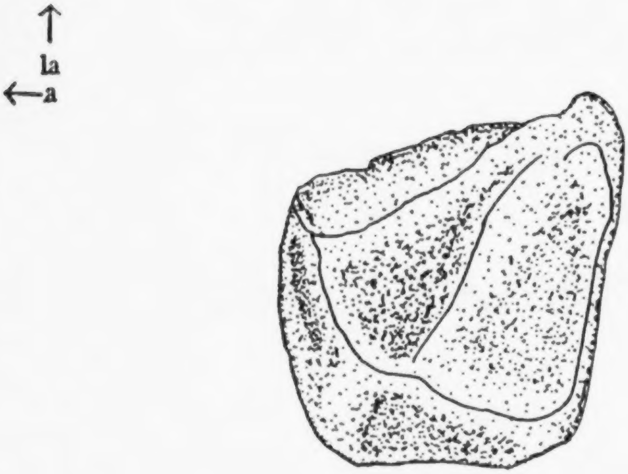


Figure 28d UALVP 34895, LM2, occlusal view, x31, *Ignacius frugivorus*.

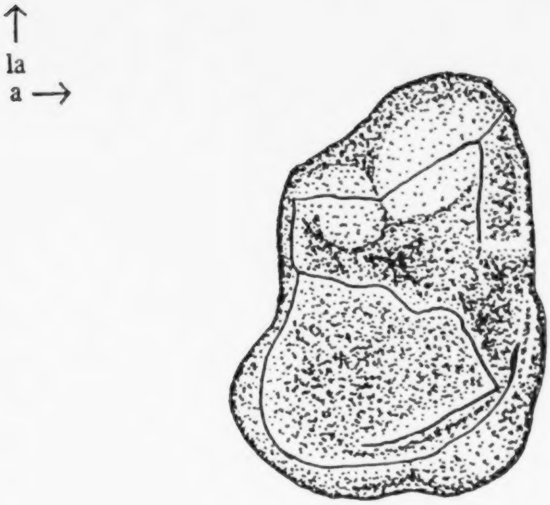


Figure 28e UALVP 34890, RM3, occlusal view, x31, *Ignacius frugivorus*.

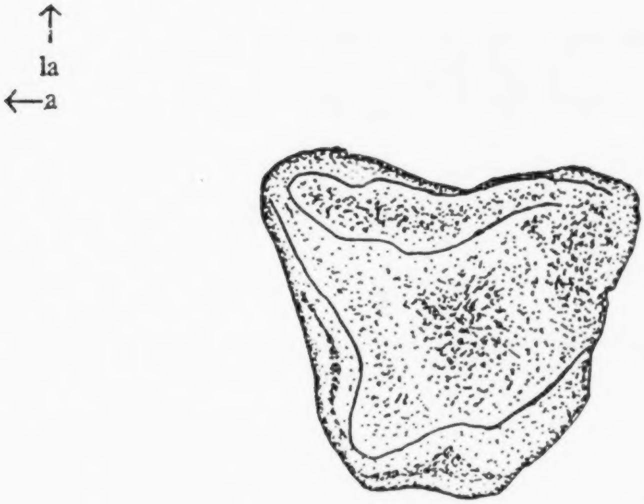


Figure 28f UALVP 34896LP4, occlusal view, x31, *Ignacius frugivorus*.

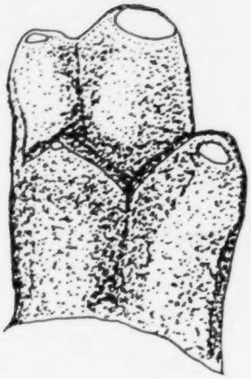


Figure 28g UALVP 34897, LI1, occlusal view, x31, Ignacius frugivorus.

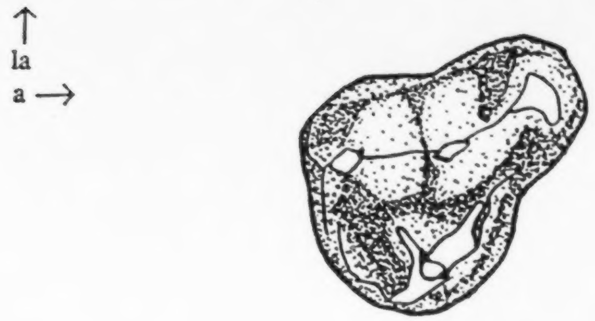


Figure 29a UALVP 34908, RDP3, occlusal view, x11, *Ectocion cedrus*.

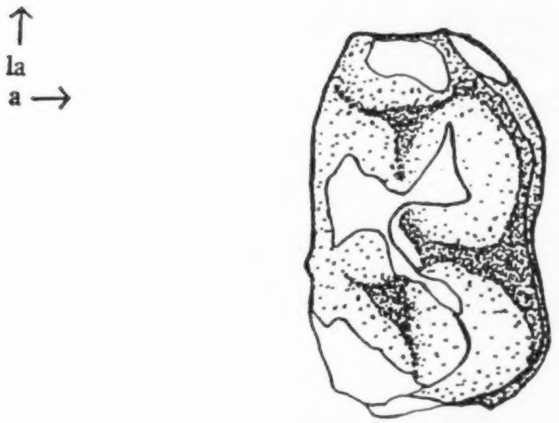


Figure 29b UALVP 34944, rp4, occlusal view, x11, *Ectocion cedrus*.

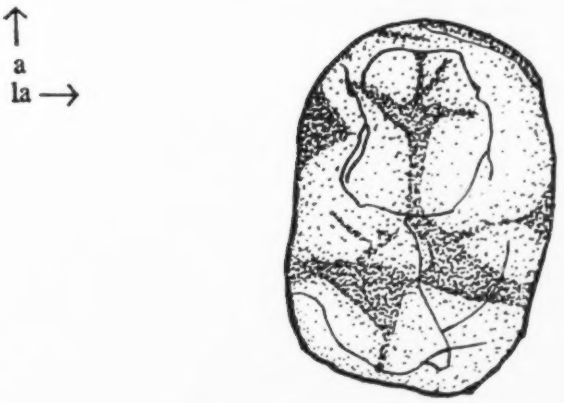


Figure 29c UALVP 34945, rdp4, occlusal view, x11, *Ectocion cedrus*.

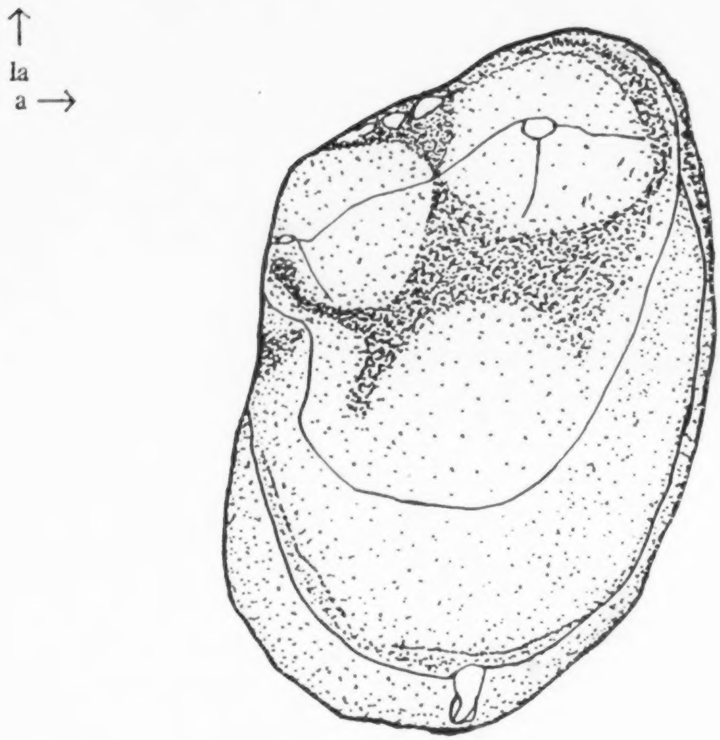


Figure 30 UALVP 34922, RM3, occlusal view, x11, *Claenodon* sp..

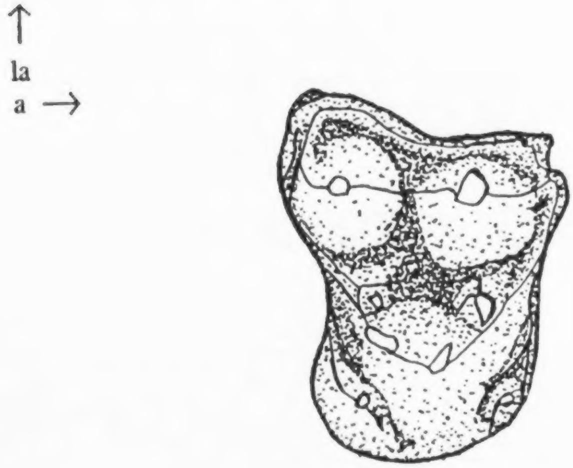


Figure 31 UALVP 35212, RM1, occlusal view, x25, *Dorraletes diminutivus*.

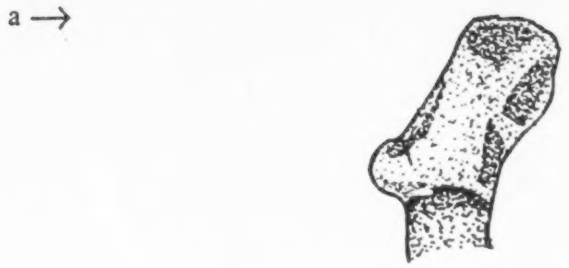


Figure 32a UALVP 35264, rp1, labial view, x25, *Elpidophorus elegans*.

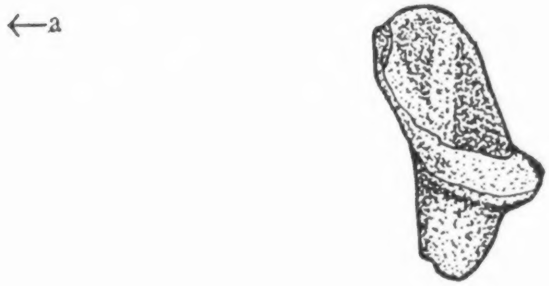


Figure 32b UALVP 35264, rp1, lingual view, x25, *Elpidophorus elegans*.

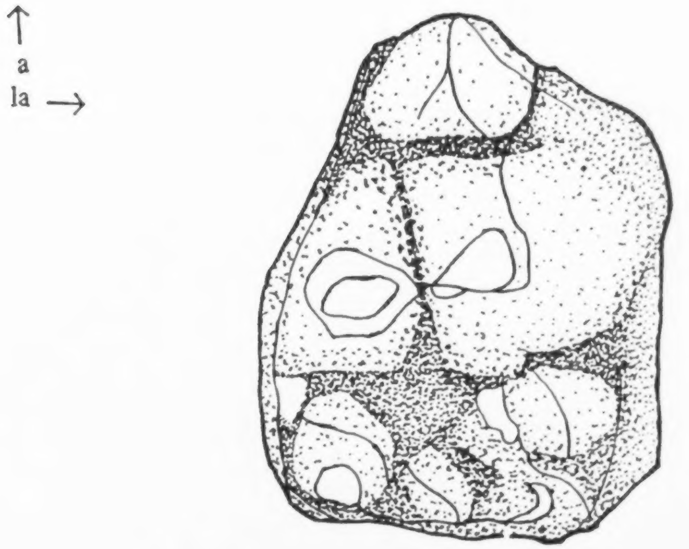


Figure 32c UALVP 35049, rp4, occlusal view, x25, *Elpidophorus elegans*.

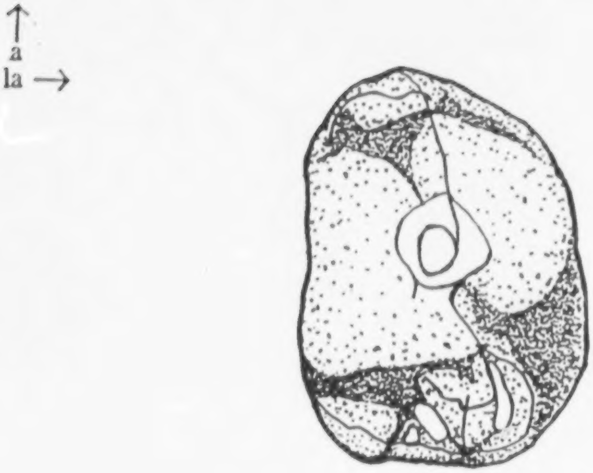


Figure 32d UALVP 35050, rp3, occlusal view, x25, Elpidophorus elegans.

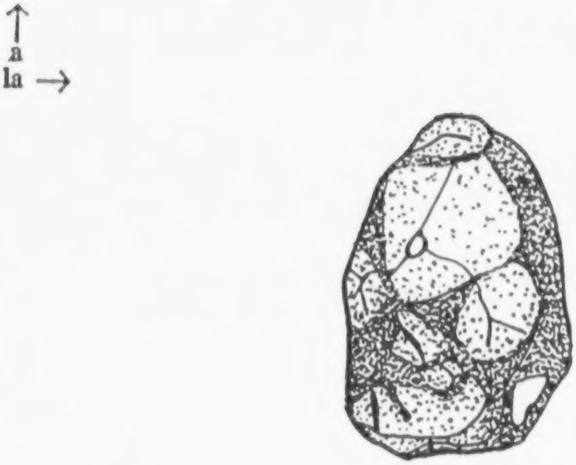


Figure 32e UALVP 35003, rdp3, occlusal view, x25, Elpidophorus elegans.

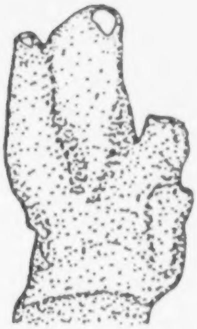


Figure 33a UALVP 35046, LI1, occlusal view, x25, Order Incertate Sedis, indeterminate genus and species.

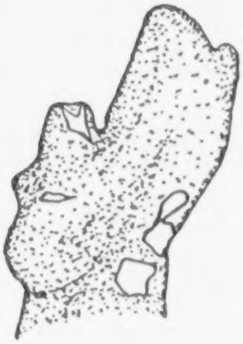


Figure 33b UALVP 35046. LI1, anterior view, x25, Order Incertae Sedis, indeterminate genus and species.

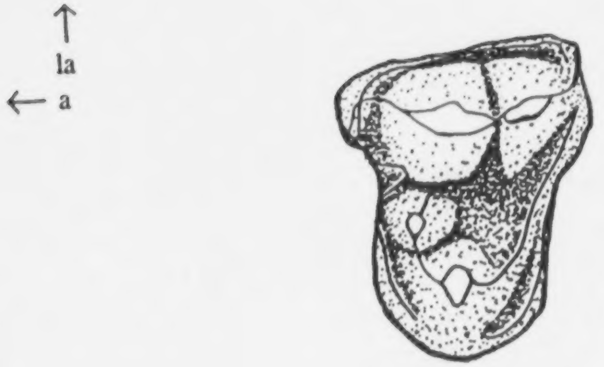


Figure 34a UALVP 35005, LP4, occlusal view, x25, *Bisonalveus* sp., cf. *B. browni*.

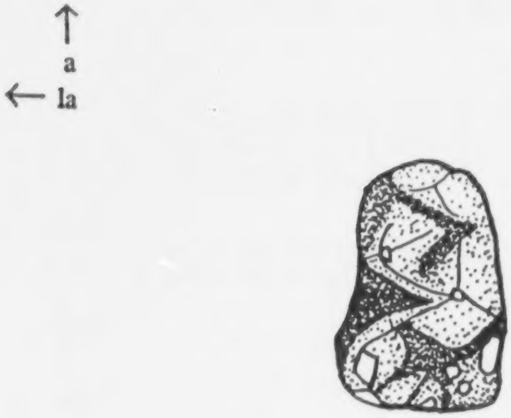


Figure 34b UALVP 35010, ldp4, occlusal view, x25, *Bisonalveus* sp., cf. *B. browni*.

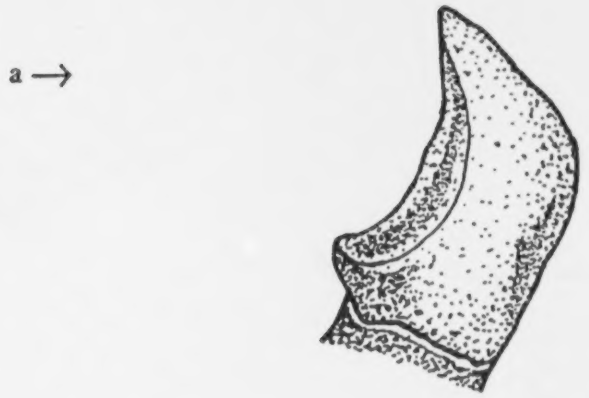


Figure 35a UALVP 35260, LI1, labial view, x25, Apatemyidae, indeterminate genus and species.

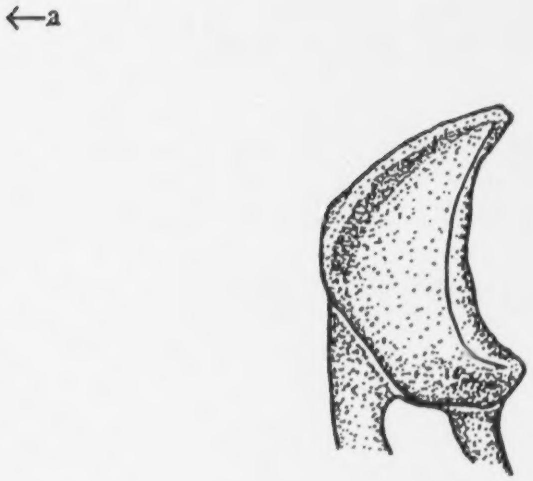


Figure 35b UALVP 35260, LI1, lingual view, x25, Apatemyidae, indeterminate genus and species.

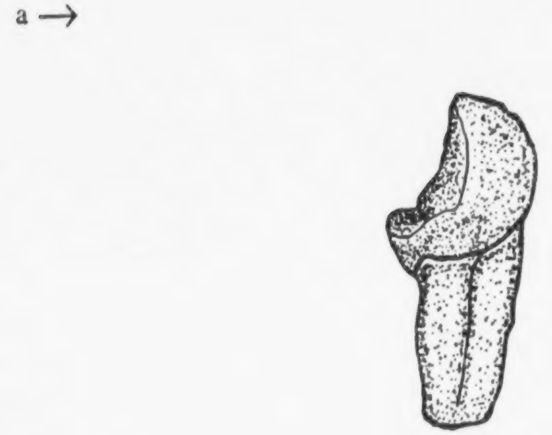


Figure 35c UALVP 35266, rp4, labial view, x25, Apatemyidae, indeterminate genus and species.

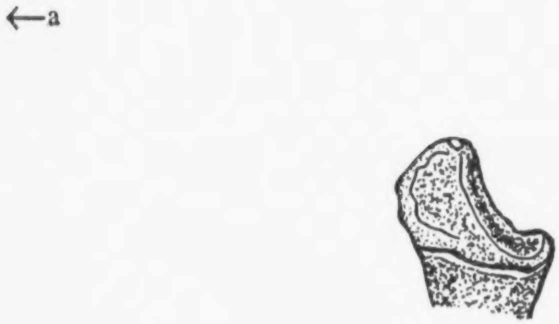


Figure 35d UALVP 35266, rp4, lingual view, x25, Apatemyidae, indeterminate genus and species.

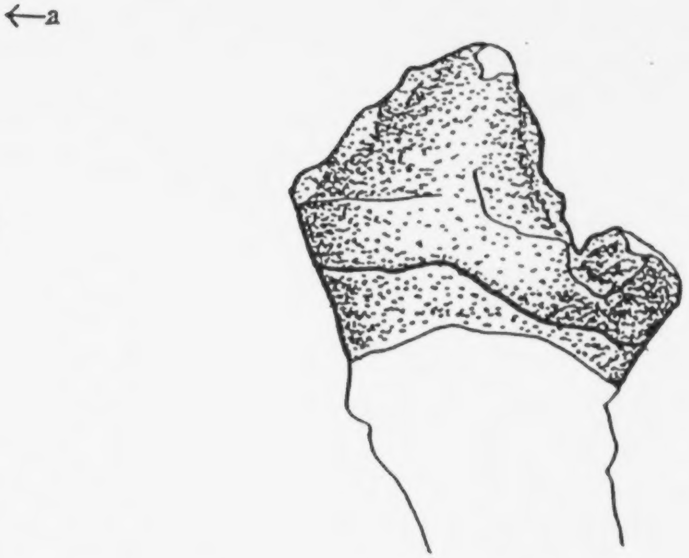


Figure 35e UALVP 35267, lp2, labial view, x25, Apatemyidae, indeterminate genus and species.

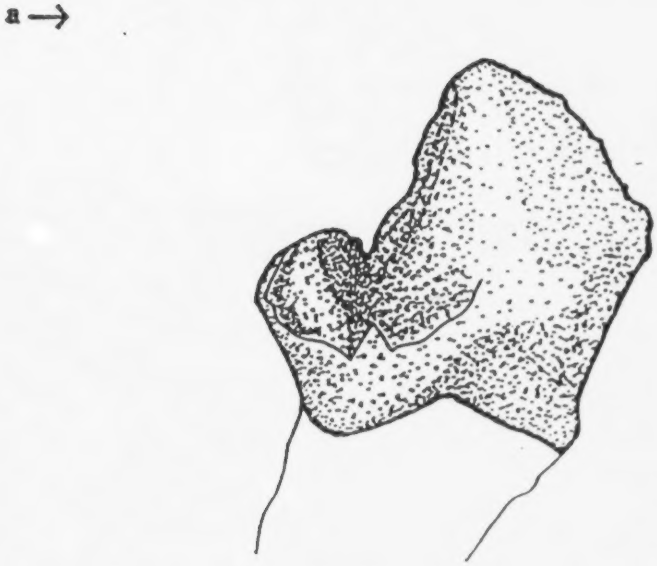


Figure 35f UALVP 35267, lp2, lingual view, x25, Apatemyidae, indeterminate genus and species.

PLATE 1

A UALVP 34889, rm2, occlusal view, x30, *Saxonella naylori*.

B UALVP 35146, LM1-M3, occlusal view, x15, *Elphidotarsius wightoni*.

C UALVP 34860, lp4-m3, labial view, x5.4, *Carpodaptes* sp., cf. *C*. *hazelae*.

D UALVP 34858, RP4-M1, occlusal view, x5.4, *Carpodaptes* sp., cf. *C*. *hazelae*.

E UALVP 34886, LDP4, occlusal view, x21.5, ?Palaecthonidae.

F UALVP 34885, ldp4, labial view, x27.2, ?Palaecthonidae.

G UALVP 35186, LDP4, occlusal view, x25.5, ?Microsyopidae.

H UALVP 35076, rp5-m3, labial view, x5.5, *Pararyctes pattersoni*.

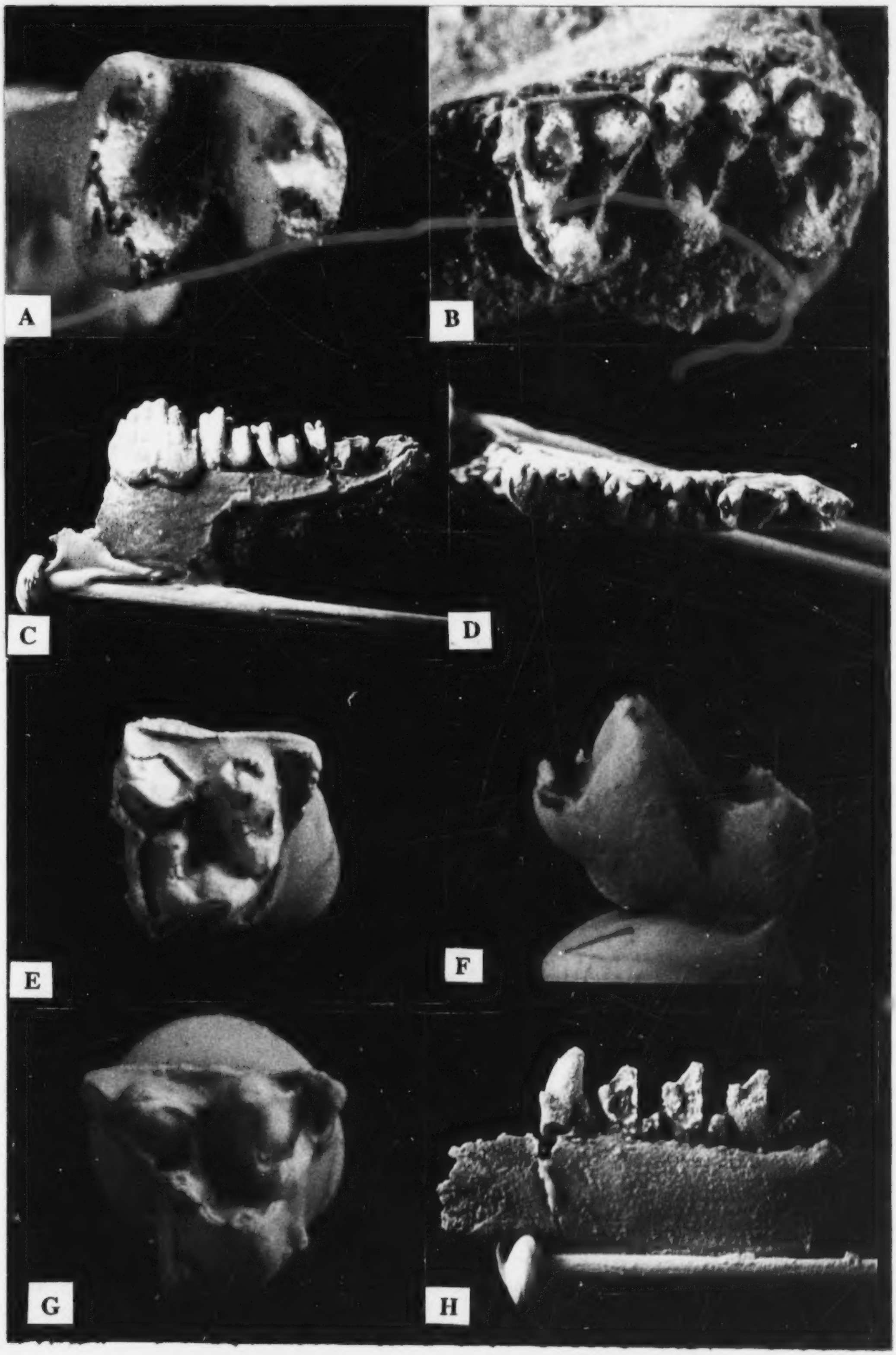

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PLATE 2

A UALVP 35156, LM2, occlusal view, x8.8, *Pararyctes* sp..

B UALVP 35153, LM3, occlusal view, x21.6, *Palaeoryctes* sp., cf. *P*. *punctatus*.

C UALVP 35154, rm1, occlusal view, x23.1, *Palaeoryctes* sp., cf. *P*. *punctatus*.

D UALVP 35113, lp3-m1, labial view, x5.9, *Litocherus* sp., cf. *L*. *notissimus*.

E UALVP 35169, lp4, m2, labial view, x3.3, *Litocherus* sp., cf. *L*. *zygeus*.

F UALVP 35169, lp4, m2, occlusal view, x3.3, *Litocherus* sp., cf. *L*. *zygeus*.

G UALVP 34929, rp2-m1, labial view, x8.2, *Leptacodon* *packi*.

H UALVP 34929, rp2-m1, occlusal view, x8.2, *Leptacodon* *packi*.

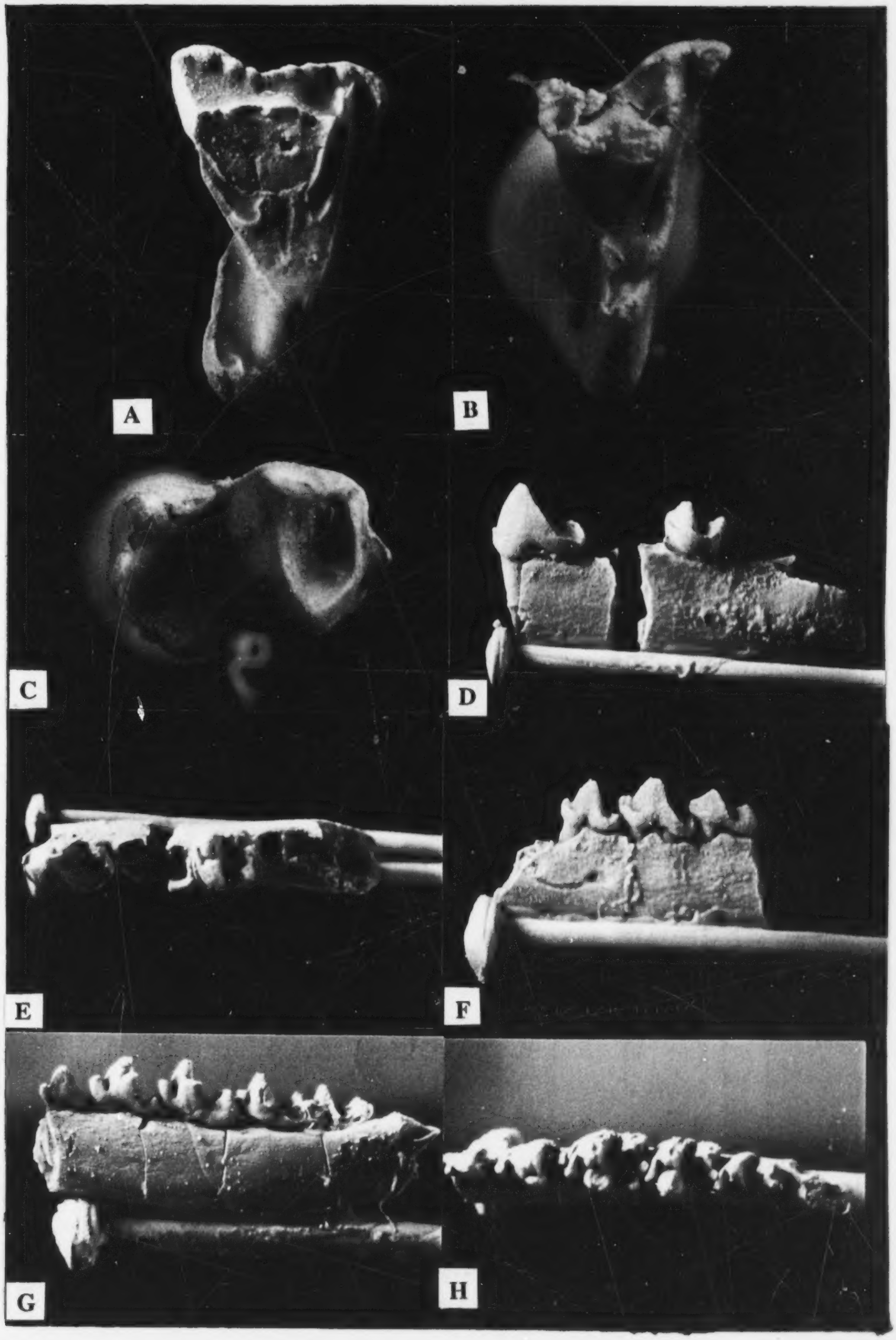
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PLATE 3

A UALVP 34939, lp1-p3, labial view, x11.2, *Nyctitherium* sp..

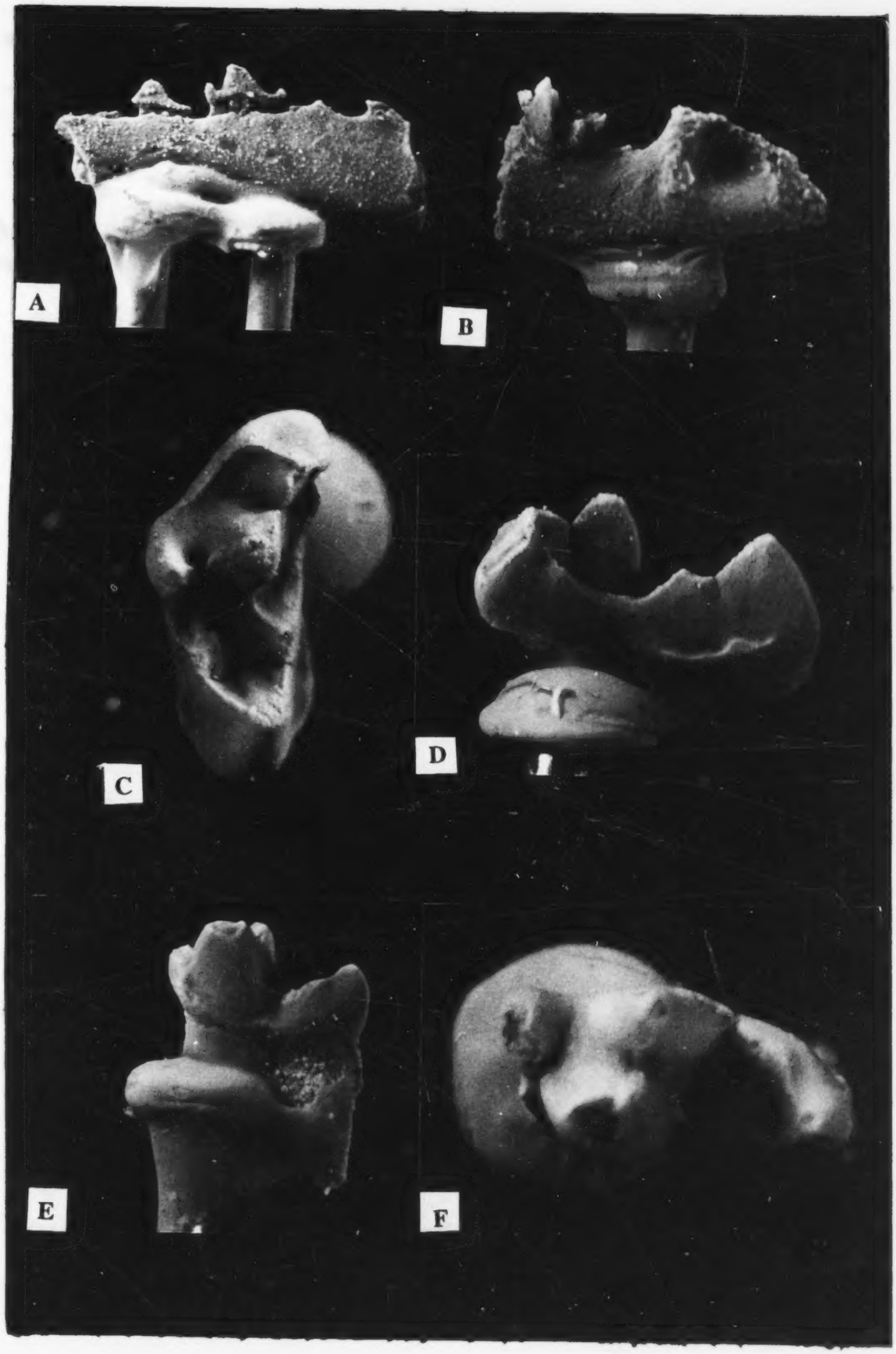
B UALVP 34933, lm3, labial view, x13.3, *Nyctitherium* sp..

C UALVP 35184, LM2, occlusal view, x16.8, *Raphictis* sp., cf. *R*. *gausion*.

D UALVP 35184, LM2, anterior view, x15.8, *Raphictis* sp., cf. *R*. *gausion*.

E UALVP 35185, lm2, labial view, x12.8, *Raphictis* sp., cf. *R*. *gausion*.

F UALVP 35185, lm2, occlusal view, x23.7, *Raphictis* sp., cf. *R*. *gausion*.


A
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APPENDIX

Whittaker's index (1972, 1977)

$$E= \frac{s}{(\log p1 - \log ps)}$$

s is the number of species, p1 is the frequency of the most common species, and ps is the frequency of the rarest species.

Shannon-Weiner index (Peet 1974)

$$H'= -\sum_{i=1}^{s} pi \ln pi$$

pi is the frequency of the ith species, and s is the number of species.

Pielou's index (1966)

$$J= \frac{H'}{\ln s}$$

Simpson's index (1949)

$$(1-L) \quad L=\sum^{s} \{ni(ni-1)\}/\{N(N-1)\}$$

ni is the number of individuals in species i, N is the total sample size, and s is the number of species.

Completeness indices (Maas et al. 1995)

$$CI= [N_{rt}/(N_t+N_{rt})]\times 100$$

N_{rt} is the number of range through genera, and N_t is the total number of genera known from an interval.

$$CI_{bda}= [N_{bda}/(N_{bda}+N_{rt})]\times 100$$

N_{bda} is the number of genera actually known before during and after an interval, N_t is the total number of genera from an interval, N_{rt} is the number of range through genera.

Standing generic richness (Maas et al. 1995)

$N_{sr}= N_{bda}+N_{rt}+1/2(N_f+N1-Nonly)$

N_f is the number of first occurrences, N1 is the number of last occurrences, Nonly is the number of genera known only fram an interval.